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Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS
ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY
JAMES JOHNSTONE, D.Sc.

XXVIII.

SAGITTA

BY

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(With 12 Plates)

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EDITOR'S PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Forty Annual Reports of the Committee and five volumes dealing with the " Fauna and Flora " have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the seashore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible station at Port Erin in the centre of the rich collecting grounds at the south end of the Isle of Man. A larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902. In 1920 the Committee ceased to exist and the management of the station was transferred to the Oceanography Department of the University at Liverpool. The name " L.M.B.C. Memoirs " is, however, still retained.

In these forty years' experience of a Biological Station, where University students and amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many University laboratories.

The objects of the Department and of the workers at the Biological Station are chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Department hopes in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following is a list of the Memoirs now published:—

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JAMES JOHNSTONE.

OCEANOGRAPHY DEPARTMENT,
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L.M.B.C. MEMOIRS

No. XXVIII. SAGITTA

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PREFACE.

From the point of view of the student of Zoology, the Chætognatha are of interest mainly because of the curious isolation of the group among the invertebrates, and because they well illustrate certain characteristics of planktonic organisms, e.g., transparency, with great delicacy of tissues; possession of "floating" devices, etc.

Sagitta is an important member of the Zooplankton and, at least for several months of the year, can easily be obtained in quantity. Students who have the advantage of working for a time at a Marine Biological Station may thus examine living specimens, and make out many of the general points in the anatomy by using low powers of the microscope and dissecting lenses. Specimens carefully preserved in weak formalin retain very well the relative transparency of the parts and may be used for examination in inland laboratories. Formalin is not good for detailed histology, and fixation in Bouin's Fluid or Corrosive-acetic mixture is recommended for this.

Sagitta is suggested as a good, if rather difficult, object upon which senior and honours students may practise embedding methods and serial section cutting. Transverse sections are the most generally useful. The head is perhaps the most interesting region, and serial sections may be used here for reconstructing the cephalic nervous and muscular systems. The sections are small and the presence of hard chitinous teeth adds to the difficulty of getting good sections, making the preparation of such a series a good test of embedding and section-cutting technique. Where economy of material, such as glassware, is to be considered, it may be noted that a complete series of transverse sections, about 4μ thick, through the head, may be placed on one 76 mm. × 38 mm. slide.

Transverse sections through the trunk, in the region of the ovaries, and through the tail, are more easily cut, and eggs and spermatozoa may be seen in various stages of development in the same animal. These form good objects for study with the oil-immersion objective, especially when Iron-Hæmatoxylin has been used for staining.

A fairly complete bibliography has been appended, which should be useful to any workers who may consult the Memoir, moreover it is advisable that senior, and particularly honours, students should be prepared to refer to original papers.

I. INTRODUCTION.

A. METHODS.

THE material used for this Memoir was obtained by means of fine-meshed silk nets. By towing such nets through the surface water of the sea, specimens of *Sagitta* may nearly always be captured, though the animal is not equally abundant at all times of the year, as will be explained later. The animals are very easily damaged by pressure, especially such delicate parts as the fins, and care is required in transferring the catch from the net to a jar of sea water. This is best done by turning the net carefully inside out and dipping it into the jar. In jars containing two to three litres of sea water, constantly renewed, *Sagittæ* were kept alive up to about twenty-four hours. Several other methods were tried in order to keep the animals alive for a longer period, but without success. Various observations were made on the living animal immediately after capture, and these were completed by the examination of specimens fixed and stained whole, and of a large number of series of sections.

The histology of *Sagitta* is minute, and the killing and fixation of the tissues is important if satisfactory results are to be obtained. If the fixing fluid be simply poured on the animals contained in a little sea water, great contraction and curling of the body follows. This may be partially overcome in two ways. One method is to transfer a specimen carefully to a glass slide, drain as much as possible of the sea water away and leave for a few seconds. If this be done carefully, the specimen will lie flat and straight on the slide. Then, holding the slide in a sloping position, suddenly flood with the fixing fluid from a pipette, running the fluid down from head to tail. The second method is especially valuable in helping the fixing fluid to penetrate rapidly into the body cavity of the animal, and thus tending to prevent the great contraction inwards, along the mid-lateral line, which occurs in Chætognatha having a strong body musculature. By this method a specimen is placed on a slide, as above, and then suddenly halved by a single transverse cut with a sharp scalpel, and immediately flooded with fixing fluid.

For a study of such features as may be seen without cutting sections, Formalin of about 4 per cent. is as good a killing agent as any. Delicate structures such as the fins are well preserved if care is taken in handling the specimens, and the relative transparency of the various parts is more faithfully retained by this agent than by any other. Alcohol is bad for this purpose.

Various fixing agents were used for the study of the histology and finer points in the anatomy. Bouin, Gilson's fluid, Picro-nitric, Flemming, Corrosive-acetic and Picro-sulphuric were mainly relied upon. Sections were cut transverse, sagittal and horizontal, usually about 4μ thick. Embedding was done in paraffin, Johnstone's rubber-paraffin, and in celloidin and paraffin. The best stain for general work was found to be Heidenhain's Iron Hæmatoxylin followed by Eosin. For making stained preparations of the whole animal, Mayer's Acid Hæmalum was found to be very good, and also Borax Carmine followed by Methyl Blue. Intra-vitam staining with methylene blue was also used, and gold or silver impregnation for the nervous system, but these latter were very capricious in action.

Hard parts, such as the jaws and teeth, were isolated by boiling out with Sodium Hydrate, and mounted in glycerine.

In order to see the "corona ciliata" in the whole animal, Fowler's method of immersing in a weak (about 0·25 per cent.) solution of methylene blue for about a minute, was found to be successful, though in some cases this structure was well seen in whole preparations stained in Hæmalum and in Borax Carmine-Methyl Blue.

In connection with the work for this Memoir, I have to thank the late Professor Sir William Herdman for much material taken on his yacht. I am also much indebted to Mr. H. C. Chadwick and Mr. Andrew Scott, for help on special points, and to Professor Cole and Professor J. Stanley Gardiner, for some specimens.

B. HISTORICAL.

Sagitta, the " Arrow Worm," was first discovered by Martin Slabber, in 1775 (97), and was placed by him among the worms. For many years after this no mention was made of this animal, and it was not until 1827 that it was re-discovered by Quoy and Gaimard (79), who gave it its present name—*Sagitta bipunctata*. In 1843, d'Orbigny (76) found five Chætognatha, which he placed among the Heteropod Mollusca. In 1844 Krohn (54) made a more detailed study of *S. bipunctata* and described the nervous system, cephalic region, etc.

Leuckart and Pagenstecher, in 1854 (62), found the general body cavity, and the first-named of these authors created the order Chætognatha, which he placed between the Nematodes and the Annelids. Two genera were recognised—*Sagitta* (Slabber) and *Spadella* (Langerhans).

Various anatomical details were described by Claparède (14), Leydig (64) and others, and in 1871 Kowalevsky (53) described the structure of the cerebral and ventral ganglia, and made the first contribution of importance to the development of the animals. O. Hertwig (45), in a well-known paper, devoted himself to the histology of the Chætognatha and the early stages of the development, and in 1883 Grassi (39) produced his general work on the whole group. In this latter work both systematics and anatomy were considered in detail, the new contributions being mainly on the spermatogenesis, the distribution of head muscles, and the structure of the intestine and fins.

Since this time many contributions have been made to the study of the order. The large number of marine collecting expeditions have added greatly to the number of species. References to these will be found in the Bibliography (e.g., Nos. 9A, 26, 27, 28, 35, 83-90, 98). On the systematics of the group the work of Fowler, Ritter-Záhony, Michael, and Germain and Joubin are especially noteworthy.

Ritter-Záhony has also produced some important anatomical work on the head region of Chætognatha, and Michael has described in detail the vertical distribution of the species found in the Californian region. Germain and Joubin have written an account of the Chætognatha collected by the late Prince of Monaco, which is published in the sumptuous style which characterises the descriptions of these collections.

The ovogenesis and spermatogenesis have been dealt with in several papers by Stevens (99-101), and Bordas (5, 6, 6A) respectively, and Bütschli (12), Jourdain (49) and Doncaster (21) have added to our knowledge of the embryology of the group.

A paper which has been somewhat neglected is that by Krumbach (56), on the jaws. These structures are about the only parts of the animals which can be preserved quite unaltered, and they are, therefore, of great importance to the systematist.

C. CLASSIFICATION.

As mentioned above, Leuckart first created the order Chætognatha in 1854, and this contained two genera—*Sagitta* Slabber, and *Spadella* Langerhans.

In 1880 Langerhans added another genus, *Krohnia*. Ritter-Záhony, in 1909 (84), pointed out that this name had been previously used by A. de Quatrefages for a genus of another group of animals, and he therefore changed the generic name and substituted *Eukrohnia* for *Krohnia*.

These three genera may be distinguished thus :—

1. Two pairs of lateral fins. Two rows of teeth on each side of the head. Lateral thickening of epidermis on body is very slight .... *Sagitta.*
2. One pair of lateral fins, partly on trunk and tail. One row of teeth on each side of the head. No thickening of epidermis .... *Eukrohnia.*
3. One pair of lateral fins situated entirely on the tail. Two rows of teeth on each side of the head. Well marked lateral thickening of epidermis extending from behind the head to tail .... *Spadella.*

The Chætognatha form a very homogeneous group, and various authors have proposed changes in the original classification, which was based mainly on the lateral fins, teeth and jaws. O. Hertwig (45) united *Spadella* and *Eukrohnia* into one genus, *Spadella*, characterised by one pair of lateral fins. Grassi (39) proposed a new classification based mainly on the character of the trunk muscles. This led to confusion and was abandoned by Strodtmann (102), who reverted to the three genera of Langerhans. P. Abric, in 1905 (1), devised a new grouping of nine genera in two large groups, based on fin characters. This method was complicated, and also included, as types, various forms which are known to be merely synonymic.

Ritter-Záhony (87) has split the genus *Eukrohnia* into *Eukrohnia* (sens. strict.), which now has three species, and *Krohnitta* with two species (one described by Oye, 76A). This author has also introduced other changes. He has created a new genus *Heterokrohnia* (90), with one species, characterised chiefly by the possession of transverse muscles in the trunk and tail. Moreover, for nomenclatural reasons, he has split the genus *Spadella* into *Spadella* (sens. strict.) with three species (one described by Johnston and Taylor, 48A), and *Pterosagitta* (Costa, 1869) with one species (88).

Germain and Joubin (32) have also made two new genera—*Pseudosagitta* and *Krohnitella*, each with one species, but Baldasseroni (3A) brings good reasons for doubting the validity of *Pseudosagitta*, and Michael (72A) agrees. Oye (76A) has recently created a genus *Zahonya* with one species.

Thus we now have in the order Chætognatha eight genera—*Sagitta*, *Eukrohnia*, *Krohnitta*, *Heterokrohnia*, *Spadella*, *Pterosagitta*, *Krohnitella* and *Zahonya*, comprising, between them, 38 recognised species. Of these, 27 species belong to the genus *Sagitta*.

The subject of this Memoir is *Sagitta bipunctata* Quoy and Gaimard, 1827. This species is chiefly characterised by the following:—Very small lateral epidermal thickening (Collarette). Anterior fin never extends as far forward as the ventral ganglion, and this fin is shorter than the posterior fin. There is always more than 50 per cent. of the posterior fin in front of the tail septum. The tail is rarely more than 25 per cent. of the total length, and there is an evident constriction at the tail septum. This species is of rather small size and its average length is nearly 1¼ cms.

D. AFFINITIES OF THE CHÆTOGNATHA.

The Chætognatha are a very difficult group for which to assign an exact position in the animal kingdom. That the difficulty is very real is shown by the fact that various workers have sought to point out affinities between this group and almost every large group of Invertebrates except the Protozoa, and in one case fanciful resemblances to the Vertebrates were described.

The group is an isolated one and all the members are very like one another. Palæontology gives no clue to their relationships. Only three entire specimens of fossils which have been referred to the Chætognatha are known (107A). These are very ancient, the formation in which they were found being Middle Cambrian. The fossils are placed in one genus *Amiskwia*, with one species *sagittiformis*. The largest specimen is 20 mm. long. A tail fin is present and one pair of lateral fins. The most interesting anatomical points in which these differ from all living Chætognaths are (*a*) the presence of a pair of strong tentacles on the head, and (*b*) the absence of a septum separating trunk and tail regions. Apart from these peculiarities the fossils appear to be fully developed Chætognaths.

Since the general characters of the living forms are of little use for determining the affinities of the group, details in the anatomy and development have to be relied upon.

Slabber placed *Sagitta* with the Vermes without discussion, but since his time the subject has been much debated. Supposed affinities with the following groups have been described :—

1. **Cœlenterates.** O. Hertwig (45) found affinities with this group mainly by a comparison of the mesenteric cavity of Actinians with the general body cavity of *Sagitta*. He also compared the nervous systems and the derivation of the muscles in the two groups.

2. **Nematodes.** Many workers have supposed affinities with this group—Gegenbaur and Hæckel among others. In both groups there is a tendency to develop cuticle, and in both there is a simple straight alimentary canal. The chief comparison which seems to be possible is between the muscular systems. The arrangement of the main body muscles in four principal bands is found in both groups, but in the histology of the muscle elements there are great differences. The vas deferens has also been com-

pared with the excretory duct of the Nematodes. In other characters the groups are, however, very dissimilar. The nervous systems are quite different; the body cavity of the Nematoda may not be cœlomic at all, and there are no longitudinal mesenteries or transverse septa in the latter group.

3. **Arthropoda.** Grassi (39) compared the cerebral ganglia of the Arthropoda and Chætognatha, and the ventral ganglion of the latter group with the ventral ganglionated chain of the former. Embryology gives no support to the suggestion that the ventral ganglion of the Chætognatha has been formed by the fusion of several ganglia. In fact, the comparison will not stand any close examination, although Patten (77A) has more recently made a further attempt.

4. **Mollusca.** Several zoologists, d'Orbigny, Siebold, Günther, Darwin and H. Milne-Edwards among others, have compared the Chætognatha with Mollusca, in most cases with the Heteropoda. Milne-Edwards, for example (68), considered the hood of *Sagitta* to represent the true head, while the portions which are ordinarily called the head he compared with the radula of the Mollusca—a mass of tissue furnished with certain hard parts forming an armature. This comparison is very fanciful, and the only points of resemblance between the two groups are to be found in the nervous system, though even here the resemblance is closer between the Chætognatha and some aberrant Annelida.

5. **Vertebrates.** Meissner (66) described a corda dorsalis beneath the brain, and therefore compared the Chætognatha with primitive Vertebrates. Later work has quite failed to show any such structure as described by Meissner.

6. **Enteropneusta.** Metschnikoff (67) united the Echinoderms, Brachiopods, Chætognatha and Enteropneusta into a group called the Ambulacraria. The main

point of the comparison was between the three segments of *Sagitta* and the three segments of Balanoglossus and its allies. More recent work has shown that the three segments of the Chætognatha are probably not homologous but have arisen in different ways, so that a comparison of the segments is not possible, and in all other characters the group is widely different from the Enteropneusta.

7. **Annelida.** Comparison with this group was naturally made at an early date. Krohn, Kowalevsky, Bütschli, and later, Huxley and Hertwig, pointed out various points of resemblance between an Annelid, e.g., Polygordius, and the Chætognatha. The main lines of the argument are as follows:—

(*a*) Both have a large body cavity and a longitudinal septum supporting the alimentary canal.
(*b*) Four groups of longitudinal muscles, pinnate in section, and with striped fibres.
(*c*) There are no circular muscles, and the epidermis is simple.
(*d*) The ventral ganglion of the Chætognatha might be considered as a concentrated nerve cord.
(*e*) Similarity between the teeth and jaws of the Chætognatha and the setæ of the Chætopoda.

As against all this the Chætognatha have no oblique septa, no nephridia and no blood vessels.

The points summarised above are based on the anatomy of the adult. Embryological investigation gives few points of comparison.

The development of *Sagitta* is very much abbreviated, and this makes the interpretation of various structures difficult. The mesoderm develops in the Chætognatha by archenteric diverticula, but by pole cells in the Annelida. There is never any stage in the Chætognatha corresponding to the trochophore of the Annelids. The segments of *Sagitta* arise differently, as pointed out above, and at different times. The posterior septum arises late in the development and is formed, according to Doncaster (21), by splanchnic mesoderm only.* Grassi put forward the suggestion that this septum was to separate the male and female genital cells, and this view is supported by Doncaster. The three segments of the Chætognathan body cannot, therefore, be compared with the Annelid metameres. A comparison of the Chætognathan genital ducts with Annelidan nephridia also seems to break down when the development of these structures is taken into account.

Thus, taking all the evidence into consideration, it is at least very doubtful if any direct comparison can be made between the Chætognatha and the Annelida.

The early stages of the development of the Chætognatha show several features which are considered to be primitive—the formation of the blastula, gastrulation by invagination, and the development of the cœlom as pouches of the archenteron. These features have suggested comparison with the corresponding developmental stages of the Brachiopods and Echinoderms, but in practically all other ways the groups differ. It is especially noticeable that no cilia are developed in the early stages of the Chætognatha, and the newly-hatched *Sagitta*, although "larval" and differing in several ways from the adult, lives at once much the same life as the latter and is the result of the abbreviated development mentioned above.

The Nematode comparison is attractive at first sight, but cannot be taken very far. The groups differ very much in the early stages of development and, as adults, the animals live under as dissimilar conditions as can be imagined. Many of the Nematodes are parasites and, no doubt, have undergone changes often associated with this mode of existence. On the other hand the Chætognatha are pelagic organisms and show a number of features usually found with this type of life.

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* The condition in the fossil Amiskwia is of interest here, see above.

It would seem as if we must go further back in attempting to get at the probable origin of the Chætognatha. According to MacBride and others, we must assume the existence many ages ago of a stock of free-swimming forms, which have been called the *Protocœlomata,* having a cœlom still communicating with the gut. All the groups of cœlomate animals have descended from this hypothetical stock, from which the Chætognatha would then be considered as a very ancient* and not greatly modified offshoot.

II. OCCURRENCE, HABITS, ETC.

Sagitta bipunctata is perhaps the most cosmopolitan of all the Chætognatha. Records show that it has been found in brackish waters, e.g., in the Zuyder Zee and in the mouth of the Para River; in coastal waters, and in the open ocean. It has been recorded in the epiplankton from all regions of the Atlantic Ocean and from the temperate North Pacific, and also in the mesoplankton in the warmer temperate and tropical parts of the Atlantic. The various stations extend from 75° N. to 34° S., and from 83° W. to 160° E. In these different localities the salinity and temperature of the water vary within wide limits, the temperature variation, for example, being from about 0° C. to over 30° C.

This wide distribution would make this animal one of the most eurythermal and euryhaline organisms known.

As against this, however, some of the records may be of doubtful value, as modern work has shown that this species has no very sharply distinguishing features, and it may be very easily confused with *S. neglecta*, *S. elegans*, and *S. setosa*, and also with the young of several other species. Thus in some of the records of the Indo-Pacific region it is possible that *S. neglecta* has been recorded as *S. bipunctata*. Neither Doncaster (22) nor Fowler (27) found the latter species in large collections made over a considerable time in this region, though a small number of immature specimens have been found by the author in " Sealark " material (Burfield and Harvey, 9A).

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* Note Amiskwia above.

In the records from the far North the reporter may have been dealing with *S. elegans* and, in connection with the low temperature in this region, it may be noted that *S. bipunctata* was not found in the far South by Jameson (47) in the Scottish National Antarctic Expedition, nor by Fowler, in the collections of the National Antarctic Expedition (28) ; neither has the present author identified this species with certainty in the large collections made by the British Antarctic Expedition (" Terra Nova ") of 1910, though many hauls have been examined. Ritter-Záhony has recently (88) re-examined this confusion of species and, in conclusion, says of *S. bipunctata* " die Art . . . . ist eine epiplanktonische Warmwasserart . . . . die ' *S. bipunctata* ' der nordischen und arktischen Meere ist *S. elegans*, teilweise auch *S. setosa* . . . ."

The temperature of the water from which *S. bipunctata* has been recorded varies from –1·7° C. to 33·6° C. The extreme low values may be incorrect for this species for the reasons indicated above. E. L. Michael (70) concludes that the optimum temperature is from 15·9° C. to 17·5° C. Recently the species has been recorded by Jameson (47), with a temperature range of 16° C. to 27° C.

The greatest depth at which this species is mentioned as having been taken with a closing net is 850-650 metres (471-360 fathoms), in Lat. 31° 25′ N., Long. 45° 52′ W., the temperature being 9·4° C. to 12·5° C.

Omitting the doubtful records from Northern waters it seems probable that about 10° or 11° C. is the lower limit of temperature at which this species has been found, as other expeditions have failed to find it at depths where lower temperatures than this were recorded.

S. bipunctata is typically an epiplanktonic form (above 100 fathoms = 180 metres), and is normally found between the surface and about 150 fathoms (270 metres). It is more often taken above 75 fathoms (135 metres), and is distinctly rarer below this depth.

This species has been considered as neritic (coastwise) in habitat, but there appear to be reliable records of this form taken too far from land to be included in this category. Ritter-Záhony (88) definitely states that this species is neritic *and* oceanic. Jameson (47), in connection with this, says that " the members of this species caught on the high seas were generally small in size and immature." The evidence at present shows that whilst large catches of this species have been made only in what may be considered as coastal waters, yet it does occur occasionally far out in the ocean.

Michael (70) has made a detailed study of the distribution of this species in the San Diego region and comes to the following conclusions :—

1. The region of 15-20 fathoms is the centre from which the species migrates or, in other words, it is the depth in which the greatest number of optimum conditions favourable to this species are found.

2. It migrates to the surface at sundown and sunrise because the conditions of light intensity at these times are *similar* to those occurring in 15-20 fathoms during the greater part of the morning and afternoon.

3. Other things being equal, it remains on the surface in greater numbers when the temperature of the water is between 15·9° C. and 17·5° C., because this is approximately the normal temperature occurring in 15-20 fathoms.

4. It remains at the surface in greater numbers when the salinity of the water is between 33·605 and 33·648 because this approximates the normal salinity in 15-20 fathoms. (This is suggested by the data, but remains to be proven.)

5. The animals leave the surface at night because the light incentive which caused them to migrate upwards is absent and they presumably return to the region of 15-20 fathoms where optimum temperature and other conditions occur.

6. Probably light has a more pronounced effect on vertical distribution than temperature or salinity because its variations are more regular and periodic

7. All individuals do not react toward light, temperature and salinity in the same way. While the majority migrate toward the surface during twilight hours, and toward deeper water during intense light and darkness, *a few almost always remain in deeper water during twilight and on the surface during intense light and darkness.* Similar individual differences occur with respect to temperature and salinity.

It is found that if plankton catches be made regularly throughout the year in one area, there is a definite succession of planktonic organisms. Data of this kind, concerning catches made with surface tow-nets in the waters around the south end of the Isle of Man, have been collected for a number of years (Herdman, etc., 43, 44, and Johnstone, Scott and Chadwick, 48c). For *Sagitta bipunctata* these records show that this animal is present throughout the year, but that it is present in maximum abundance on the surface during the day in June. The numbers then decline, but rise again slightly in October or November, and then decline again until the spring of the following year, when there is a sharp increase in May.

Michael's work shows, however, that there are definite vertical migrations during the twenty-four hours, so that the surface hauls mentioned above, taken at varying times during the day and under varying conditions, would not necessarily give correct data for the actual abundance or otherwise of *Sagitta* in the sea at the time. In view of the results of this work it may possibly be that the profusion of *Sagitta* in the surface water during the day in the summer maximum is mainly due to a temperature reaction, whereas the second increase late in the year may be more a light reaction. It is evident that light intensity, temperature and salinity all play a part in determining the presence or absence of the organism in any given locality or at any given depth.

Sagitta, when present, may be in such extraordinary abundance as to make a jar of water, into which a catch is turned, look like soup. If a catch be examined, the animals will be seen to have the appearance of colourless and transparent slips of glass which move rapidly with a darting motion. The general mechanics of the movement is probably similar to that of whales, which also have horizontal tail fins. *Sagitta* appears to undergo a very rapid bending and slightly twisting motion in the trunk and tail, and no doubt the expanse of the tail fin helps to give the necessary forward impetus. The lateral fins have no movement of their own. The whole motion is carried out very rapidly and has the superficial appearance of a shudder running down the entire animal. At the end of a forward dart the animal stops motionless and floats passively. For the floating the lateral fins will help by presenting a wide, thin, flat surface to the water.

The transparency, and the body extensions (fins) as a floating device, are both characters typical of the pelagic organisms, of which *Sagitta* is one of the more active examples.

When kept in jars the *Sagittæ* were never observed to adhere in any way to the sides or bottom of the vessel.

Sagitta is a voracious animal, and its rapid movements and series of strong hook-like jaws enable it to capture quite active prey. Its food consists mainly of floating diatoms, infusoria, copepods, and small larvae, including larval fishes. Sometimes individuals are captured in the act of swallowing another *Sagitta*, but this is not very frequent, and they are probably not normally cannibalistic. During life the animals appear to be continually opening and shutting the jaws.

Sagitta bipunctata is by far the commonest Chætognathan recorded in surface British waters, and the only other members of the group which are sometimes met with are *Spadella cephaloptera*, Busch, and *Sagitta elegans*, Verrill, the latter off the North-East coast. In view, however, of the possible confusion of certain of the species, as mentioned above, some of the British records of *S. bipunctata* may be incorrect. In these cases the correct record would most probably be *S. elegans*.

III. EXTERNAL CHARACTERS.

Sagitta bipunctata (figs. 1 and 2) is a transparent, colourless, elongated animal, somewhat spindle- or torpedo-shaped. Its average length, at maturity, is about 1·3 cms.

At the anterior end (fig. 2) is a well-marked rounded **head.** Then follows a **trunk** region separated from the head by a very slightly constricted **neck,** and the hinder part of the body narrowing gradually to the tip is called the **tail.** Around the neck region there is a slightly-thickened area where the epidermis is stratified (the **collarette,** *col.*).

The tail bears at its extremity a **caudal fin** (*c.f.*). On the sides of the body are two pairs of **lateral fins,** both placed horizontally. The anterior pair (*ant.f.*) are situated on the trunk and the posterior (*post.f.*) are partly on the trunk and partly on the tail. All these fins have supporting areas in the form of **fin rays.**

The three regions of the body—head, trunk and tail—correspond with the arrangement of the internal structures. The head itself is almost entirely surrounded by a fold of skin called the **hood.** This hood is attached along the line of the neck ventrally, and with a more anterior line of attachment dorsally (*d.hd.*), and can be drawn back to allow of the lateral divarication of the jaws, which will be mentioned again below.

Within the hood, on the head at the anterior end, are four rows of short, pointed, chitinous spines, two rows on each side. These are called the anterior (*ant.t.*) and posterior (*post.t.*) rows of **teeth** respectively. Behind these, and placed more laterally, there is a row on each side of curved chitinous hooks—the **seizing jaws** (*seiz.j.*)—attached inside the base of the hood.

On the ventral surface of the head, in an antero-ventral position, is the **mouth** (fig. 15, *m.*) and on the upper surface is a pair of small pigmented **eyes** (fig. 2, *e.*). The main mass of the head is composed of muscles having various functions.

The trunk is fairly even in outline. It is widest a little behind the middle, and tapers gradually forward and backward from this point. On the ventral surface of the trunk, about a third of its length from the neck, may be distinguished a small oval opaque area, the **ventral ganglion** (fig. 2, *v.g.*). On the sides of the trunk is the anterior pair of lateral fins (*ant.f.*) which are triangular in form.

Inside the trunk, extending through the whole of its length, the **intestine** (*int.*) may be distinguished. This opens by an **anus** on the ventral surface at the extreme hind end of this region. At each side of the intestine, at its hinder end, may be seen an **ovary** (*ov.*) appearing as an elongated opaque body. The openings of the so-called oviducts are placed laterally at the hind end of the ovaries. Immediately behind the anus there is an obvious constriction of the body, and extending across the body at this level is a septum—the **tail septum** (*t.sept.*)—separating the trunk from the tail.

The tail narrows gradually from before backwards. At the sides of the tail, behind the posterior lateral fins, is a pair of small swellings, the **sperm vesicles** (*ves.sem.*), which just touch the posterior end of these fins in mature specimens. On these vesicles are the openings of the male genital ducts. At the end of the tail is a horizontal caudal fin (*c.f.*), the posterior edge of which has a curved convex outline in undamaged specimens.

As indicated in the section on Classification, the Chætognatha form a very homogeneous group, and in attempting to distinguish between the various species, careful measurements of the salient characters are of great importance. The following table gives average values deduced from measurements of thirty to forty well-preserved specimens.* The features measured are those used by Michael (70). As in this author's tables the total length has been taken from the tip of the head to the tip of the tail fin. All the other measurements of length are expressed as a percentage of this total length. The column Posterior Fin—Tail Septum—represents the percentage of the posterior fin in front of the tail septum.

TABLE I.

				Anterior Fin.				Posterior Fin.					
Length in mm.	Width	Length of Tail.	Tail to Ventral Ganglion.	To Ventral Ganglion.	Length.	Width	To Posterior Fin.	Length.	Width.	Tail Septum.	Anterior Teeth.	Posterior Teeth.	Seizing Jaws.
13.2	6	22.6	70.4	6.5	20.4	2.1	6.6	24	3.9	59	6	13	9

* Some of the specimens were not quite well enough preserved to allow of a complete series of measurements to be made from them

The number of anterior teeth varies from five to eight, the posterior teeth from eleven to fifteen, and the seizing jaws from seven to ten. The semi-diagrammatic figure (fig. 2) has been drawn to these average measurements as seen from the dorsal surface. This figure shows the average length of this species × 10, and gives the general proportions of the animal, except that the head has been drawn somewhat large to admit of some detail being shown. The ovaries are drawn to the average size at maturity found for this species by Michael (70, p. 59).

The general appearance of these animals when viewed against a black background is, to some extent, characteristic of the species, some being more opaque in various parts than others. Doncaster (22) gave outline drawings on a black background and more recently Michael (70) and Germain and Joubin (35) have attempted to depict the relative degrees of transparency of these animals. A similar attempt for the present species is shown in fig. 1. It will be seen that the head, intestine, ovaries, ventral ganglion and seminal vesicles present a distinct contrast to the rest of the body.

It is to be noted that there is no circulatory system in *Sagitta*, and there are no localised excretory or respiratory organs.

IV. INTEGUMENT, FINS, ETC.

(i) **The Epidermis.** The epidermis consists of thin, flat cells forming a pavement epithelium with well-marked oval nuclei and evenly staining cytoplasm (fig. 4). The cells are very small in this species. The epidermis is apparently of only one layer of cells over a greater part of the body, but in certain regions it is several layers thick. On the dorsal surface of the anterior part of the head the epidermis is stratified and forms a pad of rather swollen cells (fig. 18, *sw.ep.*). At the sides of the trunk in the neck region (collarette), and on the dorsal surface of the head between the eyes (fig. 29) the epidermis is also stratified, and this is also the case along the course of the pair of large nerve commissures which connect the brain with the ventral ganglion (figs. 31, 35, *st.ep.*, and fig. 3), but the cells in these regions are not swollen. In sections intercellular spaces are seen traversed by protoplasmic strands (fig. 3, *int.c.sp.*). Over the rest of the body there is an occasional appearance of stratification. On the ventro-lateral parts of the head the cells are columnar (fig. 21, *col.ep.*).

The cells are polygonal when viewed from the surface (fig. 4), and their edges have a sinuous or toothed outline, the irregularities of adjacent cells fitting into one another so that it is difficult to isolate single cells. Over the inner surface of the Hood (fig. 24, *g.e.*), and in the Vestibular Pit the epithelium is of a glandular nature (fig. 38).

(ii) **Basal Membrane.** The epidermis lies on a structureless membrane called the *basal membrane* (fig. 3, *b.m.*). This is not very distinct in transverse sections of the anterior part of the head, but stands out as a sharply-marked line in the hinder region. It is especially thick under the glandular epithelium just inside the mouth opening (figs. 20, 21). This membrane forms a well-marked capsule around the eyes (fig. 29), and is also thickened at the sides of the neck region to form a pair of *skeletal plates* (figs. 31, 32, 33, *sk.pl.*).

A transverse section through the trunk (fig. 35, *b.m.*) shows this membrane as a thin line forming a continuous layer under the epidermis. At the attachment of the fins it forms thickened areas extending into these and functioning as skeletal supports.

(iii) **The Cuticle.** The epidermis secretes a structureless *cuticle* which is exceedingly thin over most of the body. This cuticle is thick, however, in the vestibule (fig. 16, *c.*), the depression on the ventral surface of the head at the inner end of which the mouth opens. When glandular epithelium is present, e.g., in the lining of the Hood and in the Vestibular Pits (fig. 20, *v.p.*), the cuticle is absent.

Besides this outer cuticle and basal membrane the epidermis also forms special cuticular structures in certain regions. These are the *lateral* and *ventral plates* in the head, the *anterior* and *posterior teeth*, the *seizing jaws* and the *fin rays.**

(iv) **Lateral Plates.** The pair of lateral plates each have the form shown in fig. 5. They are composed of a clear homogeneous cuticular substance, not staining with hæmatoxylin, secreted by the underlying epidermal cells which here form a very thin layer. The plates are covered by the ordinary staining cuticle. These plates lie in the sides of the head and form firm supporting structures. They have a double function—as an attaching point for various muscles, and as a support for the tooth and jaw apparatus. Their anterior slender ends sometimes extend beyond the front border of the head, giving this region a forked appearance. Their wider posterior parts diverge from one another behind. The movement of these plates helps considerably in the opening out of the jaws when the animal is attacking prey. This is explained below where the head muscles are considered.

(v) **Ventral Plates.** The ventral plates are a pair of small plates on the ventral surface of the head (fig. 29, *v.pl.*). Their anterior ends are ventro-lateral, but further back they broaden and extend up the sides. They have a similar structure to the lateral plates, and serve for the attachment of muscles on which they lie.

(vi) **Teeth and Jaws.** The teeth and seizing jaws are composed of cuticular substance similar to that of the lateral and ventral plates, and are said to be covered by the ordinary cuticle in their earliest stages. Around and beneath the base of the teeth and jaws the epidermis is composed of narrow cylindrical cells (fig. 6). This tissue extends into and fills a cavity in the centre of the teeth and jaws and forms the *pulp* (*b.p.*) of these organs.

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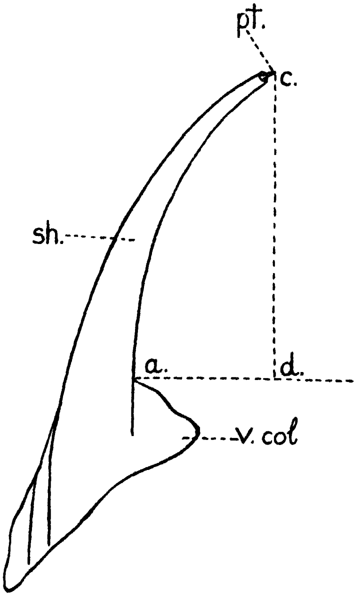
* Treated below under *Fins.*

The *Anterior Teeth* (figs. 2, 7, 14, 15, 16, 17, *ant.t.*) vary from five to eight in number on each side. In the specimen from which fig. 7 was drawn only five were present. They are all of simple sharply-conical form, and on each side form a closely-set row.

The *Posterior Teeth* (figs. 2, 8, 14, 15, *post.t.*) are from eleven to fifteen in number on each side. They have the same form but are larger than the anterior teeth, except the last three or four. They form a slightly spread-out row, the anterior members forming a curve in the vestibule, and the posterior a straight row along the border of the lateral plate. In this species the pulp of both sets of teeth appears to be absent in the adults, and to be replaced by hard substance.

The *Seizing Jaws* form a set of sharply-pointed curved cuticular rods on each side of the head (figs. 14 and 15, *seiz.j.*). The number on each side varies from seven to ten. Each set is in the form of a curved row under the hood. Their bases rest on the large lateral plates, and have strong muscles attached to them by which the jaws can be divaricated when the hood is drawn back. At rest, the jaws lie in an antero-posterior position largely covered by the hood. Each jaw (fig. 9) consists of a *base* with *dorsal* (*d.col.*) and *ventral columns* (*v.col.*) for the attachment of muscles. From this base arises a curved *shaft*, and into the top of the shaft is inserted a *point* (*pt.*). From the base, and extending up through the shaft and into the point, is the *pulp canal* containing the pulp (*p.*), which is continuous with the epidermis at the insertion of the jaw. The special characteristics of the jaws of this species are as follows. The curvature is about 40 per cent. This curvature is measured by the method described by

Michael (70). A camera drawing of the jaw is made (Text-fig. A). A perpendicular *ad* is erected on the edge of the shaft at the junction of this with the ventral column. A second perpendicular *cd* is then drawn to this line *ad* from the point *pt*. The proportion *ad/cd* measures the extent of the curvature.



TEXT-FIG. A.

The curvature along the *back* is greater than that along the *edge*, so that the apex of the point is towards the edge of the jaw (fig. 10). The point is needle-shaped and is inserted about 28 per cent. of its length into the shaft. The base of the point (*b.pt.*) and the top of the shaft (*t.sh.*) converge towards the edge of the jaw.

The pulp (*p.*) extends evenly through the canal, which is placed slightly nearer the back than the edge of the jaw. The apex of the canal lies very near the back of the point, and the canal extends into the point for about 63 per cent.

of the length of the point. In older jaws (fig 10, *sw.*) there is often a swelling in the pulp a short distance below the point.

(vii) **The Fins.** There are five fins in all, two pairs of lateral fins and a caudal fin. The position of the lateral fins on the body and their dimensions are given above. In the living animal the fins are quite transparent (fig. 1). The anterior fins are triangular in form, and the posterior and caudal fins have an evenly curved free edge in undamaged specimens (figs. 1 and 2). The fins have no muscles, and are therefore not separately movable. The lateral fins no doubt serve to balance and support the animal when floating in the water, whilst the caudal fin by its expanse helps to drive the animal forward during the rapid movement of the tail. All the fins have a similar structure. They are composed of the following parts :—

(*a*) A superficial covering of epidermis with scattered tactile organs.

(*b*) A series of fin rays.

(*c*) An amorphous basal substance.

(*a*) *Epidermis* (fig. 11, *ep.*). This forms a very thin layer on the surfaces of the fin. The tactile organs, as found on other parts of the body, are here sparsely scattered.

(*b*) *Fin rays.* The rays are easily seen in surface views of the fins (figs. 1 and 2). In the lateral fins they form parallel rows springing from the attachment of the fins to the body. The rows are not quite at right angles to the long axis of the body but slope slightly backwards. In the caudal fin they spread out fanwise from the attachment of the fin to the tip of the tail.

The study of sections of the fins (fig. 11, *fin.r.*) shows that the rays are composed of structureless substance, and are arranged in two layers, one on the upper and the other on the lower surface of the fin. The rays of the two surfaces are placed opposite one another in pairs. The rays extend outwards to the edges of the fins, where they become more slender than in the proximal portions.

(*c*) *The amorphous basal substance* (fig. 11, *b.s.*) forms a median plate of structureless material, not staining and without cells or nuclei, extending throughout the expanse of the fin. Transverse sections (fig. 40) show that this plate is thickened along the line of attachment of the fins. It here divides the dorsal and ventral longitudinal bands of body muscles in the mid-lateral line. The proximal portion of this amorphous layer stains deeply with hæmatoxylin, and thus probably has a special constitution (fig. 40, *p.b.s.*).

The fin rays appear to be embedded in the basal substance, and are probably to be considered as local thickenings of the basal membrane. The derivation of the basal substance is not certain.

V. MUSCULATURE.

Sagitta has a well-developed muscular system. The muscle fibres, so far as can be seen, are all cross striated* (fig. 12, *m.f.*). This striation can be clearly seen in the living muscle. The muscles of the trunk and tail are arranged in a comparatively simple manner, but those of the head are very numerous and their arrangement is complex. The body and head muscles will be dealt with separately.

A. Body Muscles. The trunk and tail muscles with the epidermis and basal membrane make up the body wall. The muscles lie immediately beneath the basal membrane and themselves form the lining of the body cavity in the trunk and tail. The general arrangement of these muscles can best be seen in a transverse section through the trunk (fig. 35). The fibres all run longitudinally and form six bands running down the body. Of these there are two dorsal bands (fig. 35, *d.l.m.*), right and left, two ventral bands (fig. 35, *v.l.m.*), and two much thinner lateral bands (fig. 35, *l.l.m.*) along the mid-lateral line.

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* Schneider (92) states that the muscle fibres of the visceral layer and mesenteries are possibly non-striated or smooth in character.

The structure of the fibres is peculiar and recalls the condition found in the Nematoda. The contractile portions form the outer parts adjoining the basal membrane, whilst the nuclei with a certain small amount of unmodified protoplasm form the inner parts. These inner portions form the actual lining of the trunk and tail cavities (fig. 13), no separate peritoneal endothelium being distinguishable except along the lateral line areas in the tail (see below, p. 69).

The muscles, as shown in transverse section, are regularly arranged. They consist of small fibrous plates, placed obliquely, and overlapping one another. The plates all appear to be placed in such a way that the majority are inclined at an angle of about 45° with the outer contour of the body.

The muscle bands of the body in this species are of medium thickness as compared with those of other species. The muscles in the tail (fig. 36) are relatively thicker and more powerful than those of the trunk. The contraction of the body muscles produces the rapid bending and twisting motions by which the animal propels itself forward in the water.

B. HEAD MUSCLES.* The muscles in this region have a number of different functions. The movements of the head as a whole, the movements of the teeth and jaws, the opening and closing of the vestibule and mouth, and the drawing forward and backward of the hood—all these movements are produced by special muscles.

Whilst surface views show the general arrangement of some of the larger muscles, the majority can only be successfully studied by the examination of sections cut transversely, sagittally and horizontally. Most of the muscles are shown in surface view in figures 14 and 15, and these figures should be referred to as well as those of sections, as each muscle is dealt with.

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* The muscles of the alimentary canal are dealt with below in Section VII.

In this species eighteen separate muscles have been recognised in the head and all of these except three are paired. Thus in the small head, which has an average width of about 0·5 mm., at least thirty-three separate muscles can be distinguished. In the naming of the head muscles I have followed Ritter-Záhony, who first gave an accurate description of them in *S. lyra*. For convenience these muscles may be grouped as follows, partly according to their probable functions, and partly to their position in the head.

(i) **Tooth muscles.**	1. *M. expansus superior.*
	2. *M. expansus inferior.*
	3. *M. obliquus capitis brevis.*
(ii) **Shutting jaws.**	4. *M. adductor uncinorum.*
(iii) **Constriction of mouth and vestibule.**	5. *M. constrictor oris primus.*
	6. *M. constrictor oris alter.*
(iv) **Opening of mouth and vestibule.**	7. *M. dilator vestibuli externus.*
	8. *M. dilator vestibuli internus.*
	9. *M. dilator oris.*
(v) **On upper side of the head with various functions.**	10. *M. obliquus capitis longus.*
	11. *M. obliquus superficialis.*
	12. *M. transversus dorsalis.*
(vi) **On under side of the head with various functions.**	13. *M. complexus lateralis.*
	14. *M. bicornis* (unpaired).
(vii) **Neck region.**	15. *M. transversus ventralis* (unpaired).
	16. *M. rectus colli externus.*
(viii) **Muscles of Hood.**	17. *M. protractor preputii* (unpaired).
	18. *M. retractor preputii.*

These muscles will now be dealt with in the above order, and their possible functions suggested.

1. **M. expansus superior** (figs. 14, 15, and 16 to 25, *m.e.s.*).

This is a paired muscle. The fibres have a general transverse direction, their inner ends being attached to the median connective tissue lamella and their outer ends to the front portion of the lateral plate. Their contraction would tend to draw the front ends of the lateral plates closer together, and by this action they are antagonistic to the *M. transversus dorsalis* (see below, Text-fig. B, p. 34). It appears possible that these muscles may also help in opening out the rows of posterior teeth.

2. **M. expansus inferior.**

These muscles vary in development in different species of Chætognatha. In *S. bipunctata* they cannot be sharply separated from the *M. expansus superior*, but the fibres which compose them run laterally from the median connective tissue lamella under both the anterior and posterior rows of teeth. These muscles are also probably concerned with the erection of the teeth.

3. **M. obliquus capitis brevis** (figs. 14, 16 and 17, *m.o.b.*).

These are small muscles extending between the median connective tissue lamella and the anterior part of the head. They appear to be attached to the anterior teeth and may pull them down, and so be antagonistic to the previous muscles.

4. **M. adductor uncinorum** (figs. 14, and 26 to 30, *m.a.d.*).

These muscles are visible for a considerable expanse at the sides of the head on the upper surface. Their insertions are on the ventral columns of the jaws, and their origins on the posterior part of the lateral plates. These muscles, on contraction, pull on the ventral columns of the jaws and close the latter in towards the median line.

5. **M. constrictor oris primus** (figs. 15, and 18 to 25, *m.c.o.p.*).

These muscles are inserted in the median lamella close to the *M. expansus superior*. From this point they run ventrally and outward, widening and becoming flat, band-like muscles. Their outer ends are inserted into the basal membrane at the lateral borders of the vestibule, close behind the vestibular organs. Together with the next pair of muscles they serve to close the vestibule and mouth, the front portion of the latter being pulled laterally.

6. **M. constrictor oris alter** (figs. 15, and 17 to 26, *m.c.o.a.*).

These muscles have their origins on the inner border of the lateral plate at the anterior end. From here they pass backward and downwards along the sides of the mouth and are inserted on the basal membrane just behind the previous muscles and a little to the median side of the latter. These muscles, with the *M. constrictor oris primus*, close the vestibule and the mouth, the latter being constricted to a T-shaped cleft.

7. **M. dilator vestibuli externus** (figs. 15, and 20 to 26, *m.d.v.e.*).

These muscles are inserted anteriorly on the basal membrane of the lateral border of the vestibule, just behind the vestibular organ. Each muscle is in two main portions, anterior and posterior, with the fibres running in slightly different directions. The posterior insertions are on the lateral plate between the *M. expansus superior* and the *M. adductor uncinorum*, and it is difficult to separate their fibres from those of these two muscles for a part of their course. The general action of these muscles would appear to be to widen the vestibule, and at the same time to pull back on the lateral plate and so tend to close in the jaws.

8. **M. dilator vestibuli internus** (figs. 24 to 28, *m.d.v.i.*).

These muscles run obliquely dorso-ventral; their ventral insertions are in front of the dorsal. The ventral insertion is on the inner part of the vestibule, close to the ventral insertion of the *M. constrictor oris alter*, and slightly behind the vestibular ganglion. The dorsal insertion is on the lateral plate just behind the previous muscle. These muscles also serve to open out the vestibule.

9. **M. dilator oris** (figs. 26 to 29, *m.d.o.*).

These muscles also have an oblique course. They are attached ventrally to the muscles of the mouth cavity and partly to the *M. dilator vestibuli internus*. Dorsally they are attached to the *M. obliquus superficialis* (see below). Their contraction helps to open the mouth.

10. **M. obliquus capitis longus** (figs. 14, and 17 to 29, *m.o.l.*).

The anterior insertion of these muscles is on the front of the lateral plate close to the *M. constrictor oris alter*. From this point they run backwards as well-marked bands towards the median line to posterior insertions on the dorsal wall of the head. In the hinder part of their course they run alongside the anterior portion of the *M. obliquus superficialis* (see below). The contraction of these muscles tends to shorten the head, and so possibly helps indirectly in the drawing forward of the hood.

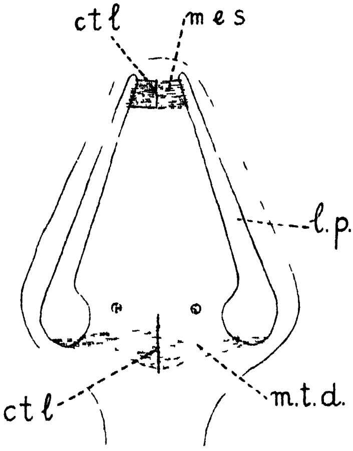
11. **M. obliquus superficialis** (figs. 14, 27 to 33, and 42, *m.o.s.*).

These two muscles are closely joined together in the median line by a connective tissue lamella (the dorsal mesentery of the œsophagus). In a dorsal view the two muscles have the shape of a triangle with a slightly curved base, the apex pointing forward. The anterior insertions are on the dorsal wall of the head behind the brain. The muscles widen rapidly posteriorly and remain attached to the dorsal body wall, wedging in between the latter and the dorsal band of trunk muscles, which they resemble in appearance in transverse section.

The function of these muscles is not very clear, but their contraction would appear to pull the head slightly upward and back on the trunk. In this way they act in opposition to the *M. rectus colli externus* (see below) in producing the nodding motion of the head.

12. **M. transversus dorsalis** (figs. 14, and 30 to 33, *m.t.d.*).

These muscles spread out laterally under the *M. obliquus superficialis*. Their median insertions are on the dorsal median connective tissue lamella. The outer insertions are on the hinder inner rounded ends of the lateral plates, and also partly on the connective tissue lamella around the *M. adductor uncinorum*.



TEXT-FIG. B.

These are powerful muscles, and their action, on contraction, is to pull the hinder ends of the lateral plates towards the middle line, and thus they probably help in opening out the seizing jaws by causing a strong pull on the muscles attached to the dorsal columns of the jaws. The *M. expansus superior* are antagonistic to these muscles, and hold the front ends of the lateral plates together (see Text-fig. B).

13. **M. complexus lateralis** (figs. 15, and 26 to 31, *m.c.l.*).

These muscles consist of many bundles of fibres mainly lying under the ventral plate and surrounding head wall. The median insertions are largely on the *M. bicornis* (see below). It appears probable that the fibres of these muscles, on contraction and expansion, determine the general form of the head.

14. **M. bicornis (and Intra-muscular organ)** (figs. 15 and 27 to 29, *m.b.*).

This is an unpaired muscle. It lies across the ventral surface of the head along the hinder border of the vestibule. Its fibres are inserted in the well-developed structureless wrapping of the muscle, and run dorso-ventrally in its median portion, but more transversely at its outer ends. The whole muscle is concave anteriorly and convex posteriorly, and also slightly concave dorsally and convex ventrally. Its lateral ends penetrate the *M. complexus lateralis.*

The whole muscle is movable and is not attached firmly to the surrounding tissues. Its function is problematical. The contraction of its fibres would alter the curvature of the posterior ventral edge of the vestibule, and the whole muscle forms a connecting link between the two halves of the head.

Embedded in the centre of this muscle is the so-called **intra-muscular organ.** This body is stated by Grassi (39) to be present in all species except *S. claparedi* (=*Spadella cephaloptera*). It consists (fig. 34) of a cell mass with indistinct outlines, but having well-marked nuclei containing granules which stain with iron hæmatoxylin. The whole structure is of an oval shape, situated in the centre of the concavity of the *M. bicornis.* In transverse section it is seen that anteriorly and dorsally this body is separated from the ventral wall of the oesophagus and the ventral œsophageal nerve by the cuticle-like investment of the muscle, while it lies against muscle fibres at its lateral and ventral surfaces. Further back it becomes entirely embedded in the muscle, although it extends back thus only for a short distance. The significance of this body is not known, and Grassi merely says that perhaps it is a nascent or vestigial organ.

A close study of sections of the head point to a possible explanation which is here suggested. In Figure 29 it will be seen that the inner portions of the muscle masses, known as the *M. complexus lateralis* (*m.c.l.*), are very clearly curved with the concavity facing ventrally. In this concavity there is a small body with nuclei similar to those described above (*int.m.org.*), and having generally the same appearance as the " intra-muscular " organ as seen in the *M. bicornis*. Thus there are similar masses of non-contractile tissue situated in the concavity of powerful muscles in each case. The peculiar position of the bodies on the strongly concave surfaces of the muscles, where the muscle fibres are not otherwise firmly attached except to their own investments, suggests that the functions of these bodies may be connected with the direction of pull on the contraction of the fibres of the muscle concerned, e.g., in the case of the *M. complexus lateralis*, or simply that they serve as a central comparatively firm supporting mass in a muscle otherwise free, as in the *M. bicornis.*

15. **M. transversus ventralis** (figs. 15, 30 to 33, and 42, *m.t.v.*).

This is also an unpaired muscle. It lies ventrally at the level of the neck and the hind end of the head. The muscle is a flat three-cornered sheet running across just beneath the œsophagus, and is attached to the body wall, being wedged in between the ventral longitudinal bands of trunk muscles. This muscle binds together the two sides of the body in the neck region.

16. **M. rectus colli externus** (figs. 14, 32, 33, *m.r.e.*).

These are very powerful muscles in this species. They run almost dorso-ventrally. Their ventral insertions are on the hinder inner surfaces of the lateral plates, and the dorsal insertions are on the skeletal plates at the sides of the neck region. Their action is to produce the nodding motion of the head, the contraction of these muscles pulling up the hind end of the lateral plate, and so tending to depress the anterior end. The *M. obliquus superficialis* acts in opposition to these.

17. **M. protractor preputii** (figs. 14, 15, and 19 to 30, *m.p.pr.*).

This muscle is unpaired and extends as a sphincter round the free edge of the hood. Its contraction draws the hood forwards and constricts its orifice.

18. **M. retractor preputii** (figs. 14, and 20 to 30, *m.r.pr.*).

This is a strong paired muscle. The median insertions are on the thick resistant connective tissue on the under surface of the brain, and the outer insertions are on the skeletal plates in the neck region. The contraction of these muscles exerts a backward pull on the hood and so acts antagonistically to the previous muscle. This pull opens out the orifice of the hood, and also aids in the spreading out of the jaws. The ventral longitudinal bands of trunk muscles also extend forwards into the hood and will help in the backward pull (fig. 31, *v.l.m.*).

VI. CŒLOM.

The **cœlom** is developed as pouches from the primitive hypoblast of the archenteron, and remains as a well-defined body cavity in the adult. In the trunk this cavity contains colourless fluid in which float a number of very small colourless corpuscles of rounded form. In the tail the cavity is largely filled with developing spermatozoa floating in the fluid.

A. Cœlom in the Head.

The cœlom appears in the head region early in development. In the adult animal the cavities can be easily distinguished in this region, with various muscles traversing it, e.g., figure 27 (*cœl.h.*). There does not appear to be any very distinct cœlomic epithelium, although on the surface of certain of the head muscles a delicate layer of " bindegewebe " can be made out, and this lies against the cœlomic cavity (e.g., figs. 28, 30, *conn.tiss.*). The head cœlom extends into the hood fig. 29).

The body cœlom also extends for a short distance into the head on either side nearly as far as the anterior end of the *M. transversus ventralis* (fig. 31, *coel.t.*). The two projecting cœlomic cavities abut against the *M. complexus lateralis* and the skeletal plate (figs. 31 and 32, *coel.t.*). The distinctive longitudinal muscles of the trunk can easily be recognised as forming a lining of these cavities, and it is to be noted that the ventral longitudinal muscle bands begin slightly further forward than the dorsal fig. 31, *v.l.m.*).

B. CŒLOM IN TRUNK AND TAIL.

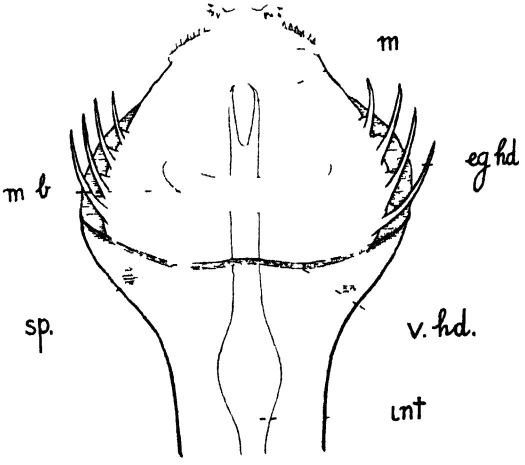
The cœlom here is spacious, and in the trunk forms a well-marked cavity around the alimentary canal. In the hinder part of the trunk the cavity is smaller on account of the ovaries lying between the alimentary canal and the body muscles. In the tail of an adult animal the cœlom is filled with masses of developing spermatozoa.

The cavities of the trunk and tail are separated by a transverse septum (fig. 2, *t.sept.*), which is said by Doncaster (21) to be formed by splanchnic mesoderm only (see also under DEVELOPMENT, p. 86). In the trunk a dorsal and ventral mesentery extend the whole way back to the hind end supporting the intestine, and dividing the cœlom here into two cavities (fig. 35). Both dorsal and ventral mesenteries are perforated here and there so that the lateral chambers are in communication. In the tail, besides the median vertical septum, there is also a secondary longitudinal septum in each of the lateral cavities (see below, p. 68).

VII. ALIMENTARY SYSTEM.

A. BUCCAL CAVITY.

The **Buccal Cavity** or **Vestibule** is in the form of a depression on the ventral surface of the head (fig. 15). At the bottom of this depression lies the mouth. In a section of the head the buccal cavity is seen to be lined with a thick cuticle (fig. 20, *c.*), under which is the ordinary epidermis of the head. The opening of the buccal cavity itself can be altered in size by the action of certain of the head muscles (see above, *M. dilator vestibuli externus*, etc.). The actual opening to the exterior on the under surface of the head is formed by the free edges of a fold called the Hood.



TEXT FIG. C. Hood from ventral surface (semi diagrammatic)

(i) **The Hood.** This is a characteristic structure of the Chætognatha and calls for a more detailed description. The hood is in the form of a continuous fold or reduplication of the skin extending completely round the head (Text-fig. C). Its line of attachment dorsally extends far forward, nearly to the anterior end (fig. 2, *d.hd.* and 14). Ventrally the attachment is further back, and lies a little behind the hinder edge of the *M. bicornis* (fig. 15). This fold is double throughout and the cœlom extends into it right up to the edge. The outer wall is formed of epidermis with cells like those of the corresponding layer of the general body, but the inner wall, which lies close against the head is composed of cubical glandular cells (fig. 24, *g.e.*). At the free edge of the hood on the dorsal surface the epithelium is glandular and the cells long and cylindrical (fig. 14, *g.e.*). Inside the cœlomic cavity of the hood there are two muscles, the *M. protractor preputii*, and the *M. retractor preputii*, the attachments and probable actions of which have been dealt with above.

(ii) **Vestibular Organ** (figs. 15, *v.o.*, and 37). This is in the form of an arched ridge lying immediately behind the posterior teeth and, therefore, situated ventro-laterally, on the antero-lateral portion of the vestibule. The free edge of the ridge has a number of blunt *papillæ* (fig. 37, *pap.*), and there is generally one papilla for each of the posterior teeth. The inner end of the ridge curves inwards and backwards towards the mouth, and the outer end has a distinct bulb-like *wing* (*w.*), beneath which is a *notch* (*no.*). Beneath the notch the ridge extends outwards and backwards as an *external process* (*ext.p.*) which may be forked. The ridge covers all but the posterior (outer) two teeth. According to Michael (70) this organ may occasionally be double on each side. In section the vestibular organ is seen to be composed of rather long cylindrical epidermal cells covered by a layer of cuticle (fig. 19, *v.o.*).

(iii) **Vestibular Pit** (figs. 15, 19, 20, *v.p.*, and 38). Situated immediately behind the vestibular organ in the vestibule there is a small round or oval depression—the *Vestibular Pit.* In section this is seen to be lined by a highly glandular epithelium, the cells of which produce an abundant cyanophil secretion. This secretion could be poured out on to the prey at the moment of seizure and possibly has a poisonous and paralysing effect.

B. MOUTH (figs. 15 *m.*, and 18 to 27).

The mouth is an oval opening situated at the bottom of the vestibule. The long axis of the oval lies antero-posteriorly. Although the edges of the mouth are not easily seen in whole preparations, a transverse section, e.g., fig. 20, shows the true mouth-opening very sharply marked owing to the immediate ceasing of the thick cuticle of the vestibule, and the beginning of the highly glandular epithelium of the alimentary canal. The mouth opening can be constricted to a narrow **T**-shape on closure, this being apparently brought about by the action of the *M. constrictor oris primus* and the *M. constrictor oris alter*, as explained above (see p. 32).

C. ŒSOPHAGUS (figs. 28 to 33, 39, 41, 42, *œ.*).

The portion of the alimentary canal situated in the head, extending from the mouth opening to the region of the neck, is called the œsophagus. Seen from below (fig. 15) the first portion of the canal is narrow, but it expands into a bulb-like swelling at the level of the hind end of the head immediately in front of the lateral diverticula of the intestine (see below). The œsophagus, as seen in transverse section, is at first somewhat rectangular in form (figs. 28 and 29), but further back becomes oval or almost circular (figs. 30 and 31).

The layers forming the wall of this portion of the alimentary canal are as follows, from within outwards :—

(i) Lining epithelium.
(ii) Basal membrane.
(iii) Longitudinal muscle layer.
(iv) Circular muscle layer.
(v) Connective tissue layer.

(i) **Lining Epithelium** (figs. 28 and 39). This consists of one type of cell of a narrow and high cylindrical form. The nuclei are basally situated. This epithelium is highly glandular and the outer ends of the cells are filled with a closely packed mass of granules of secretion staining with eosin. The secretion appears in two forms. In one kind of cell the granules are large and themselves contain smaller granules (fig. 39 *l.g.*), and in the other the granules are all very small (fig. 39, *sm.g.*). The latter cells are scattered among the former. About the middle of the head, where the œsophagus, for a short distance, is the shape of an inverted pear in transverse section (fig. 29), these glandular cells are high at the sides but much shorter on the dorsal and ventral borders. The shorter cells have the finely granular type of secretion. The cells become exceptionally high cylinders in the hinder bulb-like portion of the œsophagus mentioned above (fig. 41).

(ii) **Basal membrane** (figs. 28, and 39, *b.m.*). This stains with hæmatoxylin and forms a well-marked line as seen in transverse section. Dorsally it is connected with the vertical median partition (*dorsal mesentery*) which separates certain of the head muscles (fig. 31, *d.m.*).

(iii) **Longitudinal muscle layer** (figs. 28, 29 and 34, *m.œ.l.*). Outside the basal membrane there is a well-marked layer of muscle fibres which run longitudinally. It has been said that this layer is interrupted dorsally by a minute canal running backwards along the œsophagus, but the examination of a large number of sections failed to disclose any such canal in the present species. Ventrally, in the middle line, the muscle layer is interrupted by the *ventral œsophageal nerve* (see below, p. 49), fig. 34, (*v.œ.n.*). The *lateral œsophageal nerves* (fig. 28, *l.œ.n.*) lie at the sides of the œsophagus and, except near their origins, are embedded in this muscle layer. The longitudinal muscle layer becomes weaker further back towards the neck.

(iv) **Circular muscle layer** (figs. 28 to 31, 34 and 39, *m.œ.c.*). This layer lies immediately on the outside of the previous layer. It consists of fibres running round the œsophagus and is distinguishable as far forward as the previous layer. Immediately inside the mouth it forms a continuous layer, but its attachments in the mid-dorsal and mid-ventral lines change further back. Dorsally the attachment is first shifted to the wrapping of the *M. obliquus superficialis* (fig. 28, *m.œ.c.*), and further back the muscle becomes attached to the dorsal mesentery (fig. 31, *m.œ.c.*). Ventrally the first interruption is due to the ventral œsophageal nerve, and finally the muscle becomes attached to the *M. transversus ventralis* (fig. 30, *m.œ.c.*). The circular muscle layer extends further back than the longitudinal, and probably becomes continuous with the muscle layer of the intestine.

(v) **Connective tissue layer** (fig. 28, *conn.tiss.*). Outside the muscle layers there is a layer of connective tissue which is, for the most part, excessively thin, but shows thicker in places. Generally speaking this layer becomes thicker over the hinder part of the œsophagus.

D. INTESTINE (figs. 2, 35 and 40).

From the neck region back to the anus the alimentary canal forms a straight tube which cannot be differentiated into separate regions, and I have called the whole of this part of the alimentary canal **intestine.**

In a transverse section, through about the middle of the trunk (fig. 40), the intestine is seen to be rectangular in form with rounded corners. Further forward the canal is more oval in transverse section with the long axis of the oval placed transversely (fig. 35).

As the tube passes between the ovaries it becomes constricted along the mid-lateral line on each side (fig. 40).

The layers forming the wall of the intestine are as follows, from within outward :—

(i) Lining epithelium.
(ii) Basal membrane.
(iii) Muscle layer.

(i) **Lining epithelium** (fig. 35). The lining layer of the intestine is not relatively so thick as that of the œsophagus, and consists of two kinds of cells. There are cylindrical glandular cells, filled with granules of secretion, and having a basally placed nucleus (fig. 35, *g.c.*). These cells are similar to those of the œsophagus except that they are not so high as the latter. The second type of cell is much narrower, without granules, and these are called the " feeding " or " absorbent " cells. They have a basal nucleus and the cells appear as streaks between the glandular cells (fig. 35, *a.c.*). These feeding cells occasionally appear to be ciliated. In sections the glandular cells are often very vacuolated.

(ii) **Basal membrane** (fig. 35, *b.m.i.*). This forms a thin but continuous layer, appearing in sections as a sharp line at the base of the lining epithelium. The basal membrane in the mid-dorsal and mid-ventral line extends into the dorsal and ventral mesenteries which support the intestine, and at the attachment of these to the body wall the membrane becomes continuous with the basal membrane of the epidermis.

(iii) **Muscle layer** (fig. 35, *m.i.*). The muscle layer is very thin and appears to consist of circular fibres only. No doubt this layer is responsible for the peristaltic motions of this part of the canal. This muscle layer becomes continuous in front with the corresponding layer of the œsophagus.

Intestinal Diverticula (figs. 41 and 42, *int.div.*).

Immediately behind the head, in the neck region, a pair of lateral diverticula can often be seen in whole preparations, and more especially in the living animal, in which this part of the intestine is generally in movement with a kind of gulping action, probably largely due to the contractions and expansions of the head. Horizontal sections (fig. 41) indicate that these diverticula (*int.div.*)

extend forward to a point immediately behind septum (*sept.*) between head and trunk. Transverse sections through this region show the diverticula clearly (fig. 42, *int.div.*). The central canal has a lining epithelium exactly like that of the œsophagus, and a series of sections shows that this central region is simply a dorsal and ventral backward continuation of the œsophagus. The pair of lateral diverticula, on the other hand, have the typical lining epithelium of the intestine, and can be traced back in continuity with it. Thus it appears that the œsophagus has grown back in a dorsal and ventral prolongation, and that the intestine has grown forward in two lateral prolongations. These regions, meeting and fusing, give rise to the diverticula.

As to the possible function of this arrangement, the strong expansions and contractions of the head muscles must exert considerable alternate pulling and compressing actions on this anterior portion of the intestine. The folding forward of the intestine on either side would allow of a certain amount of lengthening of the alimentary tube in this region by the pulling forward of the backward prolongation of the œsophagus, and so opening out a part of the fold. It can easily be seen in the living animal that the strong expansion of the head on the seizing of prey does result in the pulling forward of this region of the intestine.

Anus (fig. 43, *an.*).

The intestine opens posteriorly by a ventrally situated oval anal opening. This opening lies just in front of the transverse septum which limits the trunk behind. A vertical longitudinal section through this region shows that just inside the anal opening the lining epithelium of the intestine is a little different from the general intestinal epithelium described above. Here it consists of a single layer of shorter cylindrical cells forming a columnar epithelium. These cells are of the absorbent type, not glandular. This epithelium ceases at the aperture, and immediately outside this we see the general epidermis of the body. Close around the anal aperture the basal membrane of the epidermis is thickened. No special sphincter muscles could be distinguished, and the action of the trunk muscles in this region, together with the circular muscles of the intestine and a natural elasticity of the tissues around the opening, are probably sufficient for the opening and closing of the aperture.

E. MESENTERIES (see also under CŒLOM above, p. 37).

The intestine for the whole of its course is supported in the mid-dorsal and mid-ventral lines by a pair of very thin mesenteries. These mesenteries (figs. 35 and 40, *mes.*) when seen in transverse section, are shown to consist of a median basal membrane which is continuous on the one hand with that around the intestine and on the other with the basal membrane of the trunk wall. On each side of this membrane there is a very thin muscular layer. When the surface of a mesentery is examined it is seen that the fibres of this layer run dorso-ventrally.

These mesenteries are perforated at intervals, so putting the cœlom on the two sides into communication. There are more perforations in the ventral than in the dorsal mesentery. Thus the parietal layer around the intestine, consisting of basal membrane and muscle layer, is continued into the mesenteries, and so to the somatic layer lying under the epidermis.

The septa in the tail region are mentioned below when dealing with the male generative organs (see p. 67).

VIII. NERVOUS SYSTEM.

The **Nervous System** consists of a brain and several ganglia in the head with a number of nerves, and of a large ventral ganglion in the trunk connected with the brain by a pair of commissures. The ventral ganglion gives off a number of nerves to the trunk and tail regions, the branches of these nerves constituting the peripheral nervous system.

The portion of the nervous system situated in the head will be considered first. All the nerves in the head are paired, with one exception to be mentioned below.

A. THE BRAIN, GANGLIA AND NERVES OF THE HEAD (fig. 44; also see sections figs. 16 to 30, 45, 46, 51 and 53).

(i) **The brain and cerebral nerves.** The brain, seen from above, is a body of quadrangular form lying close under the dorsal surface of the head about half-way between the eyes and the anterior end of the animal (fig. 44, *b.*). In a specimen 1·5 cms. long the brain measured ·2 mm. wide × ·15 mm. long. The anterior portion of the brain is enclosed in a layer of rather large bladdery cells (the "Mantelgewebe"), which tends to form a thickened mass dorsally (fig. 18), though this is not so marked in this species as in some others, e.g., *S. hexaptera.*

Anteriorly are given off a pair of *Frontal* or *Anterior Commissures* (figs. 44 to 46, 53 and 16 to 19, *f.c.*), which arch outwards and downwards and join the *Vestibular Ganglia* (figs. 44, and 21 to 25, *vest.g.*). These latter form a pair of very large ganglia lying ventro-laterally at the sides of the mouth. The vestibular ganglia are connected with one another by an *Œsophageal Commissure* (figs. 44, 26 and 27, *œ.com.*), which runs slightly backward and beneath the œsophagus, and joins the vestibular ganglia on their inner surfaces.

It will thus be seen that these portions of the nervous system—Brain, Frontal Commissures, Vestibular Ganglia, Œsophageal Commissure—form a ring around the anterior end of the alimentary canal (fig. 44).

From the brain, besides the frontal commissures, are given off the main commissures, optic nerves and coronal nerves, all of these being paired.

The *Coronal Nerves* (figs. 44, 45, and 26 to 29, *co.n.*) spring from the hinder border of the brain near the middle line and run back at first just beneath the basal membrane of the epidermis (fig. 28). They pierce the basal membrane at about the level of the eyes, and are distributed under the modified epidermis of the ciliated ring.

The *Optic Nerves* (figs. 44, 45, 46, and 26 to 28, *o.n.*) arise from the brain slightly behind and to the outer sides of the coronal nerves, and also at first lie under the basal membrane. This membrane forms a capsule round the eyes (see below p. 60) and the nerve pierces this and enters the anterior end of the organ. The nerve then divides into two main branches (fig. 29, *o.n.*), which diverge from one another and encircle the inner eye structures.

The *Main Commissures* (figs. 44, 45, 53 and 25 to 33, *m.c.*) arise from the lateral borders of the brain to the outer side of the frontal commissures. Within the brain they are connected together by a narrow transverse band of fibres (fig. 45). The main commissures are enclosed at first in a layer of the " Mantelgewebe," but soon leave this and pass out under the basal membrane into the hood (fig. 27, *m.c.*). In the region of the neck the commissures pierce the basal membrane and enter the epidermis, which in this region consists of several layers of cells (figs. 35, *m.c.* and 42). Thence they pass back gradually into the trunk epidermis and round to the ventral surface, where they finally enter the Ventral Ganglion (figs. 47, 48, *m.c.*).

(ii) **Vestibular Ganglia, Œsophageal Commissure and their nerves** (fig. 44). Close to the point at which the frontal commissure joins the vestibular ganglion there is given off laterally a nerve, the *Frontal Nerve* (fig. 19, *f.n.*) which runs to the posterior teeth. At the origin of this nerve there is a small *Frontal Ganglion* (fig. 20, *f.g.*) which can hardly be distinguished in this species from the vestibular ganglion. On the frontal commissure, just before the latter joins the vestibular ganglion, there arises a nerve, the *Œsophageal Nerve* (figs. 17 and 18, *œ.n.*), which runs first inwards towards the œsophagus and then backwards in the wall of the latter where it is known as the *Lateral Œsophageal Nerve* (*l.œ.n.*). At first this nerve is embedded in the circular œsophageal muscle layer (fig. 21, *l.œ.n.*), but further back comes to lie deeper in the longitudinal muscle layer (fig. 24, *l.œ.n.*). On this nerve, before it reaches the œsophagus, there is a stout ganglion, the *Œsophageal Ganglion* (figs. 19 and 20, *œ.g.*). From the dorsal surface of the vestibular ganglion a large nerve arises which runs dorsally and then backwards in the *Expansus Superior* muscle beneath the lateral plates. This is called the *Dorsal Nerve* (figs. 21 to 30, *d.n.*). This nerve continues back into the *dilator vestibuli internus* muscle (fig. 26, *d.n.*), and still further posteriorly it is lost in the *M. adductor uncinorum* (fig. 30, *d.n.*). On the way back it gives a small branch ventrally to the *M. dilator vestibuli internus* (fig. 26, *nv.*).

From the vestibular ganglion other small nerves also arise. Of these the two which can be most easily followed are :—

(*a*) A nerve which passes out dorso-laterally just in front of the *M. dilator vestibuli internus* and appears to run to the seizing jaws (fig. 24, *md.nv.*). I have called this the *Mandibular Nerve.*

(*b*) A *Vestibular Nerve,* which arises more ventrally from about the middle of the vestibular ganglion (figs. 23 to 25, *v.n.*). This nerve runs downward and outward to the border of the vestibule, which it reaches between the *M. constrictor oris primus* and the *M. constrictor oris alter* at the level of the posterior insertion of the first-named muscle.

From the œsophageal commissure there arises an unpaired nerve, the *Ventral Œsophageal Nerve,* in the mid-ventral line (figs. 28, 29 and 34, *v.œ.n.*). The nerve runs backward in the musculature of the œsophagus and finally passes more ventrally into the *M. transversus ventralis*. This nerve appears to be paired in the hinder part of its course, as if it had divided into two branches (fig. 30). The œsophageal commissure also gives rise, just in front of the hinder border of the mouth, to a pair of very small *Labial Nerves*, on each of which there is a very minute ganglion (fig. 44, *lab.n.*).

B. THE VENTRAL GANGLION AND ITS NERVES (figs. 1, 2, and 47; also see sections figs. 48 and 49).

The *Ventral Ganglion*, as seen in surface view, has an elongated oval shape, the long axis being antero-posterior. The length of the axes in an individual 13·5 mm. long were ·78 mm., and ·30 mm.

In side view the ganglion forms a distinct projection. The position of the ganglion with reference to the tip of the tail and to the anterior fin is given above (see table, p. 21). This ganglion is connected in front with the brain by the two large *Main Commissures* (fig. 47, *m.c.*) mentioned above, which, coming down from the brain, enter the ganglion at its anterior end.

From the lateral borders of the ganglion there arise a number (about twelve) of paired nerves (*l.n.*) which run close beneath the epidermis. These nerves branch, and the branches connect with one another and form a network distributed mainly to the back and sides of the trunk. From the posterior end of the ganglion a pair of larger nerves arise (fig. 47, *p.n.*). These also divide and branch and form a network which is distributed over the hinder part of the trunk and tail regions.

C. PERIPHERAL NERVOUS SYSTEM (fig. 50).

This is the plexus of nerves which arises, as described above, from the nerves given off from the ventral ganglion. The plexus lies just beneath the epidermis and appears to be distributed all over the trunk and tail regions. The fibres become excessively fine and are joined at intervals by short fine anastomosing branches. Here and there in the plexus are ganglion cells (*gang.c.*). It would appear that the fibres of this system innervate both the muscles of the trunk and tail, and also the sensory touch organs which are scattered over the body

D. HISTOLOGY OF THE NERVOUS SYSTEM.

(i) **The Brain and Cephalic Ganglia.** The brain is embedded in the epidermis of the dorsal surface of the head and slightly projects on the surface, forming a flattened hump. Sections show that over the dorsal surface of the brain is the delicate basal membrane of the epidermis, and this membrane also forms a layer on the ventral surface (fig. 46, *b.m.*), so that the brain is entirely enclosed by the membrane except where nerves and the median portion of the retrocerebral organ pass through it. Within the capsule thus formed the brain is seen to consist of a central fibrous mass, the "*Punktsubstanz*," and a more superficial layer of nerve cells. Outside the nerve cells there appears to be a thin investing layer (neurilemma). The "*Punktsubstanz*" seen in section (figs. 23, 24, 46, *b.pnkt.*) has a finely dotted appearance with an occasional fine striation. This no doubt indicates that this portion of the brain consists of a mass of fine nerve fibres forming a network.

The general form of the central mass of fibres may best be seen by examining a series of longitudinal sagittal sections. Such a section cut along one of the large frontal commissures (fig. 46) shows an anterior mass of fibrous substance passing to the frontal commissure anteriorly, and separated from a more posterior mass by a dorsal groove filled with ganglion cells. The anterior mass represents a section of a large transversely placed band of fibres which connects the proximal ends of the two frontal commissures together (fig. 45). The posterior mass is the main body of " *Punktsubstanz.*" This is larger and extends further dorsally than the frontal commissure connection.

A longitudinal section along the mid-dorsal line (fig. 51) shows the main fibre mass extending across the whole height of the brain, and the cross connection of the frontal commissures is now seen as a relatively much smaller body in front, the dorsal groove between these two being filled with ganglion cells, and much deeper than in the section previously described.

The central mass of fibres is seen in transverse section in figure 24. The appearance of a separate small portion of this tissue above the main mass and separated from it by a thin layer of ganglion cells (as seen in figures 21 and 22), is due to the fact that the front part of the dorsal surface of the head curves downward to a slight extent; thus the more anterior sections are cut slightly obliquely through the brain. The small upper portion of fibres is the upper anterior part of the main fibre mass.

The Ganglion Cell layer is composed of nerve cells with their processes and supporting tissue. The cells have fairly well defined outlines (fig. 52), with clear or slightly staining cytoplasm and large round nuclei containing dot-like deeply staining chromatin bodies. This layer is found between the origins of the two frontal commissures at the anterior end of the brain (figs. 19, 45, *gang.c.*). Just behind this level the ganglion cells form a layer completely investing the " *Punktsubstanz,*" although the layer is of unequal thickness. It is thickest dorsolaterally and extends into the depression between the cross connection of the frontal commissures and the main mass of " *Punktsubstanz* " as described above. Ventrally it consists only of a few scattered cells forming a very thin layer (fig. 20). Further back even this thin layer disappears and the fibre mass is in contact with the basal membrane lamella except for the very thin neurilemma (figs. 22, 46).

Behind the level at which the pair of main commissures is given off the cell layer is seen to extend more ventrally between these commissures and the central mass of "*Punktsubstanz*" (fig. 25, *b.g.*). A short distance further back the central fibrous mass ends, and a transverse section of the brain then shows a mass of the nerve cells in which are embedded the *coronal* and *optic nerves* and the lateral parts of the *retrocerebral organ* (fig. 26).

Cephalic Ganglia. These are similar to one another histologically, and the structure can best be seen in the large vestibular ganglia. We have in these a structure similar to that of the brain. There is a central mass of "*Punktsubstanz*," and around this a layer of nerve cells with fibres (figs. 21 to 25, *vest.g.*). The nerve cells in these ganglia are mainly concentrated on the median side. The whole is surrounded by a delicate sheath (fig. 25).

(ii) **The Retrocerebral Organ.** Several authors, Busch (10), Kowalevsky (53), Grassi (39), have described an organ situated at the hind end of the brain in the mid-dorsal line. That the structures found in this position are very small and easily overlooked is shown by the fact that Hertwig (45), in spite of his careful work on the Chætognatha, makes no mention of any organ here.

Grassi described a median dorsal depression, "fossetta retrocerebrale," opening on the surface in the middle line just at the hind edge of the brain, and a pair of "appendici" embedded in the hinder lateral parts of the brain.

Schneider (92) described the median portion (fossetta), which he called the "neuroporus kanal," as seen in longitudinal sagittal section. He compared the finer structure of this canal with that of the touch organs of the body. This author also described a pair of canals in the anterior part of the brain, but the presence of these has not been confirmed. He thought that all these canals resulted from the method of brain development, and that the brain was really a hollow structure.

Ritter-Záhony (82) briefly mentions Schneider's organ, and gives one longitudinal section of the brain which shows this organ as in Schneider's figure. This author also mentions that he observed a dark blue pigment at the anterior end of the " corona ciliata " in living *S. bipunctata*.

Recently Kuhl (56A) has studied this organ in detail in *S. elegans*, and his description has been confirmed in the main for *S. bipunctata*. I believe this author is correct in treating Grassi's " fossetta " and " appendici " as one organ, and I retain the term *Retrocerebral Organ* for the whole body.

In the living specimen the outer opening of the organ can easily be found on careful examination. This is a transversely placed oval situated in the mid-dorsal line at the hind edge of the brain. The opening is filled with a very fine clear granulation, and the anterior border of the corona, which passes across the head close behind the opening, does not seem to be connected with the latter in any way. This is the only part of the organ which can be distinguished in the living animal. I have not been able to find the pigment mentioned by Ritter-Záhony. Whole fixed and stained preparations and sections show further details of structure.

A whole preparation seen from the dorsal surface (fig. 53) shows the outer opening of the organ (*r.c.op.*) surrounded by two rows of nuclei, and at the lateral hinder quarters of the brain are seen the pair of appendages (*r.c.gl.*). The latter stain less deeply than the nuclei of the nerve cells of the brain.

A horizontal section (fig. 45) through the brain shows the relations of the appendages of the organ more clearly. These appendages (*r.c.gl.*) are now seen to be a pair of club-shaped bodies embedded in the mass of nerve cells at the hinder lateral corners of the brain. Each appendage is clearly marked off from the surrounding nerve tissue by a membranous or slightly fibrous covering, in which an occasional nucleus can be distinguished.

The appendage itself is seen in section to be divided into a number of chambers by very thin septa, the chambers containing finely granular lightly staining material similar to that found in the dorsal opening. On the walls of the chambers can occasionally be seen very small oval nuclei. Transverse (fig. 26, *r.c.gl.*) and sagittal sections (fig. 46, *r.c.gl.*) show these compartments of the appendages well.

The appendages become narrowed behind near the mid-dorsal line, and each passes into a short tubule which is circular when cut in transverse section. These tubules open dorsally into the external opening of the organ. The external opening is well seen in longtitudinal sagittal section (fig. 51, *r.c.op.*). The opening is somewhat funnel-shaped, and it pierces the epidermis of the head. The nuclei of the epithelium forming the walls of the funnel stain deeply and have a similar form to those of the corona. The opening is filled with a mass of clear, and presumably secretory, material. No nerve connecting the retrocerebral organ with the brain can be discovered, although there may be a connection with some of the brain ganglion cells in the region of the external opening, in which position Kuhl has described some peculiar spindle-shaped bodies.

Most authors who have studied this organ ascribe to it some unknown sensory function. Kowalevsky compared it with the "touch organs," Grassi with the "corona." Patten (77A), in the pursuit of his theory of the Origin of the Vertebrates from the Arthropod stock, says that it represents the "parietal eye" of the Arthropod.

The structure of the organ in the adult Chætognathan does not clearly indicate that it is a sensory body, and some knowledge of its development, together with a study of the organ in living specimens of some large form, e.g. *S. hexaptera*, would probably throw more light on the question. In the present state of our knowledge it does not seem to serve any useful purpose to make what must be merely guesses at its possible function.

(iii) **The Ventral Ganglion.** Flat stained preparations (fig. 47) show that this ganglion consists of a central mass of fibres (*fib.m.*) and a border of ganglion cells down each side. The central fibrous portion is composed of fibres running along the length of the ganglion and also fibres running across at right angles to these.

Transverse sections are the best for showing the finer structure of the ganglion (figs. 48, 49). Such a section taken through about the middle of the ganglion (fig. 49) shows that it is covered ventrally by a thin layer of the ordinary trunk epidermis (*e.p.*), while dorsally it is covered by the basal membrane of the epidermis (*b.m*). Thus the whole ganglion is embedded in, and is derived from the ectoderm of the animal. In the centre is the somewhat flattened cylinder of "*Punktsubstanz*" (*fib. m.*), while laterally is the well-marked layer of ganglion cells on each side (*gang.c.*). These cells are somewhat smaller than but similar in appearance to those of the brain and cephalic ganglia. In the general mass of ganglion cells some larger ones can be distinguished situated in the more lateral part of the nerve cell layer. Fibrous prolongations can frequently be seen running inwardly towards the "*Punktsubstanz.*" A few ganglion cells can also be found in the mid-ventral line. Figure 48 shows the main commissures (*m.c.*) cut in transverse section just as they enter the ventral ganglion.

IX. SENSE ORGANS.

A. Tactile Bodies (figs. 19, 54 and 55).

Scattered over the surface of the trunk and tail of the animal there are small projections situated in the epidermis. From each of these little hillock-like bodies there projects a bunch of very fine stiff hairs which are almost invariably lost on preservation and can only be made out by careful examination of living specimens. These bodies are considered to be sense organs, and from their structure Gegenbaur (31) supposed them to be tactile in function, an opinion with which other workers on the group agree.

These organs are fairly evenly distributed over the body. They are found in the space within the ciliated ring (see below), and may be present even on the proximal portion of the fins. In a favourably stained whole preparation (Mayer's Hæmalum is good for this) the organs can be clearly made out in surface view, and it is then seen that they tend to be arranged in longitudinal rows down the body, and also in fairly definite transverse rings around the trunk and tail. The average number is about 250 arranged in six or seven longitudinal rows. In surface view the bodies are seen to vary somewhat in exact size and shape in the same animal. Some are oval and others circular, and in the former case the long axis may be parallel with the longitudinal axis of the body or at right angles to this. In whole stained preparations the nuclei of the cells of the tactile organs are contrasted with those of the ordinary epidermis cells and the limits of the organs are easily seen (fig. 54, *nu*'.). In lateral view the organs are also sharply defined (fig. 55). Such a view shows that each organ is made up of a number of closely packed narrow cells, each with a deeply staining nucleus (*nu*'.) These cells lie on the ordinary pavement epithelium of the epidermis (*ep.*). From each organ there spring a number of stiff hairs as mentioned above (*h*). These hairs project, not from the whole surface of the organ, but as a closely arranged regular row from the central cells only. These rows of hairs are arranged in the transverse axis of the animal. In the centre of each organ there is a small pit containing a non-staining homogeneous body (*pit*). The remaining cells of the organ differ slightly in their staining reactions from the hair-bearing cells, and the latter are no doubt the true sensory elements, whilst the former are of the nature of supporting cells. Probably owing to the excessive fineness of the fibres no actual nerve supply could be traced to the organs, but there does not seem to be much doubt that at least the hair-bearing elements have a nerve supply from the peripheral system. Grassi (39) gives two figures [Tav. VII, figs. 11 and 12] showing such a connection.

B. CILIATED RING (CORONA CILIATA) (figs, 56, *co.* 57).

This organ is situated wholly on the dorsal surface of the animal on the head and trunk, and is in the form of an unpaired closed ring of modified epithelium. The actual shape of the ring varies in the different species of Chætognatha, and in the present species it is very elongated in the longitudinal axis of the animal. The whole organ is very delicate and in some preserved specimens cannot be found at all. In favourable preserved and stained whole preparations the nuclei of the modified cells are sharply defined as in those of the tactile bodies mentioned above, and it is then seen that in this species the organ has the form of an elongated ring with a very slightly sinuous outline (fig, 56). The anterior boundary of the ring is situated immediately behind the brain and the organ extends back between the eyes well on to the trunk. In a specimen of 1·5 cms. long the longitudinal and greatest transverse axes of the ring were 1·8 mm. and 0·2 mm. respectively.

A surface view of a stained preparation (fig. 57) shows that the ring consists of a double row of modified cells, the nuclei of which are sharply contrasted with those of the surrounding epidermis. Each row is three or four cells in width. Careful examination of living forms reveals the fact that these cells have very delicate cilia which are constantly kept in motion. The cilia are entirely lost on preservation.

There is not much doubt that we have here a sensory organ, for not only does the form of its cells indicate this, but there is in this case a well-marked nerve supply direct from the brain in the form of the pair of stout *Coronal nerves* (figs. 26 to 29, 44 and 45 *co.n.*). The origin and distribution of these nerves are described above (see p. 48). The fibres of these nerves can be traced to the ciliated cells. The question as to what sense this organ subserves is much more debatable, as is often the case with the sense organs of invertebrates. The function usually ascribed to them is that of smell (Hertwig), or taste (Grassi), but these are hardly more than guesses, and have little to support them beyond the form of the cells with their delicate cilia.

C. EYES (figs. 2, 14, 29, 58, 59, 60).

There are two well-marked eyes situated on the dorsal surface of the head a short distance behind the brain. The eyes are placed on the outer sides of the ciliated ring, and in an average specimen are about 0·2 mm. apart. Naked eye examination shows the eyes as a pair of black spots, but the use of a low power objective of the microscope on a whole preparation reveals the fact that the eye really consists of a *central pigmented area*, the " nuclear region " of Grassi, and a surrounding *unpigmented region*, the " cortical region " of the same author. The whole eye viewed from the surface is circular and has a diameter of about 0·1 mm., and it is quite sharply marked off from the neighbouring tissues.

Only four workers have considered the structure of the eye in any detail, Hertwig (45), Gourret (38), Grassi (39) and Hesse (45A). Of these Hertwig and Grassi gave considerable detail, but did not agree as to all the points of structure. Hertwig concluded that there were three lens-like bodies in the pigmented portion, and that the clearer rod-like structures, which are easily seen surrounding the pigmented part, were the actual rods of the visual cells touching the lenses. Grassi thought that there were three "retinulae," each composed of three layers, an outer layer of supporting cells, then a layer of sensory cells, and finally an internal layer of rods, "coni bastoncini," the latter coming up against the centrally placed pigment. Both these authors derived their observations principally from a study of a large Chætognathan, *Sagitta hexaptera*. Grassi states that in smaller species he could not clearly distinguish two zones of cells in the outer "cortical" region of the eye. This author considers the eyes of Chætognatha as structures *sui generis*, not to be compared directly with those found in various other invertebrates, but as having a special structure and physiology. Hesse, who has carried out a great deal of work on the eyes of invertebrates, is the latest to deal with the eye in the Chætognatha. This author also worked mainly with *S. hexaptera*, and his interpretation of the eye structure differs from both Hertwig and Grassi. Work done for this Memoir on *S. bipunctata* confirms, in general, Hesse's conclusions, although in this small species it is difficult to be quite certain as to the exact arrangement of the smaller elements.

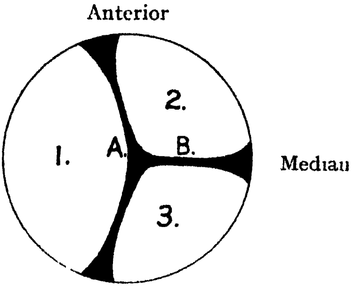
The whole eye has the form of a sphere flattened dorsoventrally so that it appears oval in transverse and longitudinal sagittal sections. The eye structures are enclosed in a very thin membrane in which small nuclei can be seen. Outside this is a firm capsule formed by the basal membrane of the epidermis (figs. 29, 59, *b.m.*). On the upper surface of this capsule there is a very thin layer of epidermis. The *Optic Nerve* has been described above (see p. 48) This nerve enters the anterior border of the eye capsule, and then divides into fibrillæ which pass into the inner portion of the organ (fig. 58 *o.n.*).

Sections cut transversely, horizontally and sagittally show that the central portion of the eye, in which lies the pigment (nuclear region of Grassi), has a somewhat complicated structure.

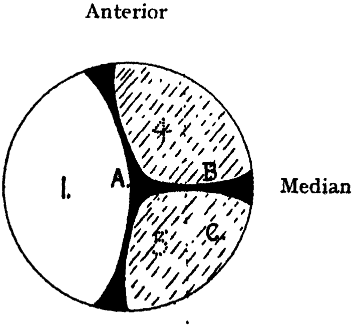
Surface View of " Nuclear " Region. In surface view the pigmented part of the eye in fresh preparations has the general shape of a circle, but the lateral half of the circle is less darkly pigmented than the median half, in which the internal structure is obscured by dark brown or black pigment (fig. 58). Gourret was unable to find any further structure in this median portion, but both Hertwig and Grassi described certain " partitions " as existing in this part, although their descriptions do not agree in detail. These " partitions," in spite of the general pigmentation of the " nucleus," can be seen on careful examination of dorsal and lateral views as black lines, distinguishable from the dark brown of the rest of this portion. Hesse's work has cleared up doubts as to the precise structure, and it is clear that the " partitions " represent the walls of five pigment cups arranged in a particular manner.

Sections of the " Nuclear " Region. Thin sections should be cut transversely, horizontally and sagittally. The arrangement of the pigment cups is best explained with the aid of a series of diagrams (Text-figs. D–I).

(*a*) *Horizontal sections.* The uppermost sections show the " partitions " as in surface view, and as shown in Text-fig. D. Here we have three pigment cups, the walls of the cups appearing as dark brown or black " partitions " in the sections. Of the three cups shown here one (numbered 1) is evidently considerably larger than the other two, and is laterally placed. The other two cups are of equal size and face medianly. Of these the anterior is called No. 2 and the posterior No. 3. The common pigment wall between cups 1 and 2 and 3 is called *A*, and the common wall between cups 2 and 3 is called *B*. About the middle of this series of sections the appearance is as shown in Text-fig. E. Here the pigment walls *A* and *B* are still shown, but *B* is less distinct, because the whole of the median half of the " nucleus " is pigmented brown. Here then, it is clear that there is a *horizontally* placed pigment wall at about the level of the equator of the sphere. This wall is called *C*. The wall *C* evidently represents the ventral wall of the cups 2 and 3. Sections cut still more ventrally return to the first appearance. Thus beneath the wall *C* there are two more pigment cups



TEXT-FIG. D.

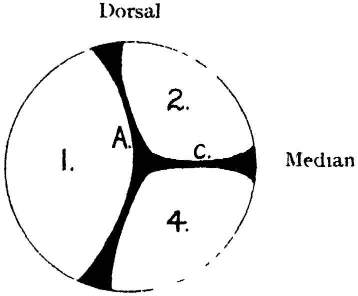


TEXT-FIG. E.

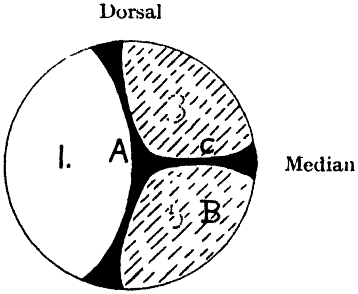
similar to Nos. 2 and 3. These are numbered 4 and 5. Of these No. 4 lies beneath No. 2, and No. 5 beneath No. 3.

Throughout the series the large lateral cup, No. 1, presents the same appearance.

(*b*) *Transverse sections.* The most anterior transverse sections have the appearance shown in Text-fig. F. If the above interpretation of the structure be correct, it will be evident that here we are seeing the pigment walls *A* and *C*, and the three pigment cups shown will be Nos. 1, 2 and 4, the latter pair being the more anterior of the median set of four small cups. Further back the appearance becomes as in Text-fig. G. This is superficially similar to Text-fig. E, but it will be clear that now the general brown pigmentation of the median half of the nucleus is due to the cutting of the wall *B* parallel to its



TEXT-FIG. F.

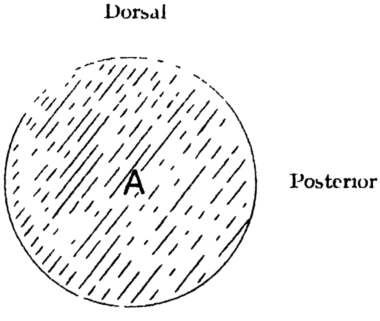


TEXT-FIG. G.

surface. Still further back the sections revert to the appearance of Text-fig. F, but the median side we are now seeing the two posterior cups Nos. 3 and 5.

In this series again cup No 1 does not change its appearance

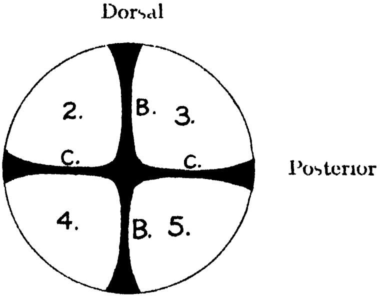
(c) *Longitudinal vertical (sagittal) sections.* Taking a series of sections from the outer side towards the median line of the animal, the first sections show no pigment walls. This would be expected as we are simply cutting across the cavity of the outer large cup No. 1. In the middle of the series, however, the whole section becomes pigmented as in Text-fig H. This section will be cutting the pigment wall *A* parallel to its surface. Still further towards the median side we shall have a condition of the pigment walls not seen in sections cut in the other planes. Such a section may be imagined as cut down through the dotted line shown in Text-fig. E. It will be seen that we shall have the pigment walls *B* and *C* both cut in transverse section, and the appearance is now as in Text-fig. I. The two walls here show as a cross, since they both extend completely across the " nucleus " in this plane. The cross can be seen when the whole eye *in situ* is examined from the side. This curious appearance of the eye was neither mentioned nor figured by Hertwig or Grassi. We now see the four median cups 2, 3, 4 and 5. It was the missing



TEXT-FIG. H.

of this appearance which led both Hertwig and Grassi to the erroneous conclusion that there were only three main portions in the " nuclear " region.

Thus the sections show that the eye consists of five pigment cups lying with their walls closely applied to one another, so that these appear as pigmented " partitions." That these cups are closely joined is shown by the fact that the whole of the " nuclear " region of the eye can be moved as a distinct body from its natural position. When the eye is depigmented with acid alcohol, the walls of the cups show in sections as a clear substance with very faint striation. Of the five cups the largest faces laterally, and the four smaller face inwards, two above and two below.



TEXT-FIG. I.

The Sensory Cells. Associated with each of these cups is a group of visual cells (figs. 59, 60) which almost entirely fills the cavity of the cup, and also the space between the cup and the enclosing capsule. The outer ends of these cells each contain a well-marked, deeply staining nucleus (*nu*), and beyond the nucleus, i.e., further from the pigment cup, the cells each narrow to a fibre (fig. 60, *f.*), which comes into close relationship with a fibre of the optic nerve. The fibres of the nerve can easily be seen in surface view of the whole eye coming very close up against the outer ends of the visual cells, and it is possible, though it could not be clearly seen, that the fibrous extensions of the visual cells actually form the optic nerve fibres. These outer parts of the visual cells, together with the optic nerve fibres, form the greater part of the " cortical region " of Grassi.

The inner part of each visual cell passes into a rod body (*r*) which lies in the cavity of the pigment cup. Each cup is almost completely filled by its collection of " rods." In the living animal they are strongly refracting and often exhibit a faint pink colouration. These rods are present as separate bodies in the cup, but both Hertwig and Grassi supposed that they fused, and it is a group of rods which Hertwig called a " lens." In the living animal these rods are not easily seen, except some of those belonging to the lateral cup, because of the pigment. Within the inner ends of the visual cells, between the nucleus and the rod, there is a clearer area, conical in form, the base of the cone being inwards and passing into a rod, and the apex of the cone pointing towards the nucleus (fig. 60, *cl.r.*). These areas stain fairly deeply at the apex end, and here appear to pass into a fine fibril which runs outwards through the cell, and finally passes out as the fibril of the visual cell mentioned above. The clear inner ends of these structures in the visual cells are strongly light refracting, and lie up against the openings of the pigment cups. Thus they are clearly seen in a surface view of the living eye, and have a superficial appearance of a layer of clear rod-shaped bodies. It is these structures which Hertwig took for a layer of " rods " of the " retina," and he thought that they were placed with their inner ends against the " lens." According to the above description they are portions of the visual cells passing into the true rods which lie inside the pigment cups.

General Physiology of the Eye. The eye of *Sagitta* is a combination of five pigment-cup ocelli. The rods would appear to be the light-sensitive elements, and from these, when stimulated, a nerve impulse would pass outwards through the fibrils and along the optic nerve to the brain. It will be noted that the arrangement of the elements is such that it is the outer fibril ends of the visual cells which are directed towards the incoming light. Thus the eye may be said to be inverted. There is no difficulty about the light reaching the inner four pigment cups, as all the tissues of the head are transparent. It is evident that there can be no image perception in this type of eye, but the organs no doubt serve to distinguish light intensity, and there will be a limited sense of directional perception.

The structure of the eye gives no great help in fixing the phylogeny of the Chætognatha. Similar simple pigment-cup ocelli are found in various other invertebrates—Platyhelminthes, Nematoda, the median eye of some Crustacea, some water living Annelids, e.g., Ophryotrocha, Tomopteris, and the eye of various larval forms such as the nauplius and trochophore.

X. REPRODUCTIVE ORGANS.

Sagitta is a hermaphrodite animal. The female organs and ducts are situated in the trunk segment and the male in the tail.

A. The Male Reproductive Organs.

(i) **Tail Cavities and Septa** (fig. 36). The cœlomic cavity in the tail extends from the transverse septum situated immediately behind the anus, back to the hinder extremity of the animal. This cavity is widest in front and gradually narrows as it passes backward. It is completely divided into two by a median vertical septum (fig. 36, *v.sept.*), resulting in a right and a left chamber exactly comparable to one another. This septum is seen in section (fig. 61) to consist of a median homogeneous layer continuous in the mid-dorsal and mid-ventral lines with the basal membrane (*b.m.*) underlying the epidermis. On each surface of this layer another layer can be seen forming the actual lining of the cavity on the median side (*e.v.sept.*). This layer in transverse section has the general appearance of a simple epithelium of cubical cells with large nuclei. These cells are probably ciliated, but no definite anatomical evidence could be obtained of this. Among the cells of this layer, deeply placed, there can also be seen bodies which have the appearance of muscle fibres.

Sections show that the anterior ventral part of this septum divides a short distance behind the intestine into two layers which curve outwards and forwards and join the transverse septum (fig. 62, *v.sept.div.*). This can also be seen from the surface in good, whole preparations (see Text-fig. J). In the middle line between these two divisions of the median septum, the transverse septum curves backwards. Thus it comes about that the hind end of the intestine lies in a small space limited behind by the transverse septum and the divisions of the median tail septum.

There is also to be seen in transverse section a secondary longitudinal septum in each chamber, lying parallel with the median partition, and dividing the anterior portion of each lateral chamber into two equal parts (fig. 36, *sec.sept.*). This secondary septum is excessively thin, and although in a transverse section a nucleus can occasionally be seen on its surface, especially near its dorsal and ventral attachments, no other structure in the septum itself could be made out. The septum is attached dorsally and ventrally to the inner lining of the tail cavity muscles, and extends from close to the transverse septum in front to about the level of the seminal vesicle behind.

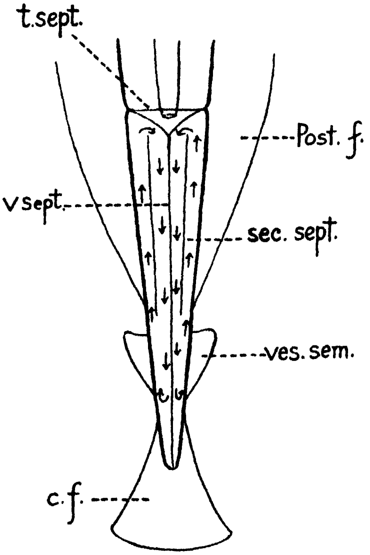
The outer wall of the tail cavities is composed of the same layers as that of the trunk, with which it is continuous—

epidermis, basal membrane, and longitudinal muscles. No inner lining epithelium can be distinguished here except on the lateral line behind the testes. In this posterior part of the lateral line there appears to be an epithelium similar to that forming the surfaces of the median longitudinal mesentery. In the region of the vas deferens this epithelium of the lateral line area is several cells thick (fig. 36, *lat.l.ep.*).

The transverse septum consists of a median homogeneous layer, and on the anterior and posterior surfaces of this a few nuclei can be made out, so that there is probably a very thin cellular covering.

(ii) **Testes.** There are two testes, one in each chamber of the tail. Each testis is a solid body which lies in the anterior part of the tail cavity attached to the outer wall in the region of the lateral line area and ventral longitudinal muscle band. Viewed from above, the testis appears as a band of cells extending from the transverse septum to nearly the hind end of the median fin. The band is broader in front than behind, and at its anterior extremity runs for a short distance towards the middle line parallel to the transverse septum. Each testis is covered by a thin layer of endothelium continuous with the body wall along the line of attachment.

From the testes there are continually being budded off masses of round sperm-mother cells. These cells then undergo their growth and maturation stages whilst floating in the fluid which fills the tail cavity, so that this cavity is found to be filled in adult animals with masses of sperm cells in various stages of development. These developing spermatozoa are kept in continual movement in the tail cavity, presumably by the action of ciliated cells of the lateral line area and median septum. The movement is one of circulation. In each chamber of the tail cavity the sperm masses move forwards on the outer side, pass round the anterior end of the secondary septum and then backwards alongside the median longitudinal septum (Text-fig. J). Bordas (5) says that the movement of the round spermatocytes is caused simply by their being pushed about by the actively-moving ripe spermatozoa. If this be so it is difficult to account for the regular circulatory movement. Moreover, small isolated masses of spermatocytes were observed to move very rapidly when close to the median longitudinal septum in a manner which leaves little doubt that the surface of this septum is ciliated.



TEXT-FIG. J.

(iii) **Vasa deferentia** (figs. 36, 63). These ducts, through which the spermatozoa pass to the exterior, are found one on each side of the tail segment. The ducts are relatively long, extending from the hind end of the testis back to the sperm vesicles, which are situated just in front of the root of the tail fin. Each duct has a very small bore and opens internally at its anterior end into the tail cavity by a round or oval opening having slightly thickened lips. This opening is situated in the dorsal part of the lateral line area (fig. 63, *int.op.vas.def.*). The tube runs back from this point without convolutions, embedded in the body wall of the lateral line area (fig. 36, *vas.def.*), and opens behind into the front end of the sperm vesicle, passing outwards through the lateral body wall as it does so. This posterior opening of the vas deferens is slightly more ventral in position than the anterior (internal) opening, so that the tube slopes ventrally a little on its way back. The duct is lined throughout with a simple epithelium, which is in two layers at the thickened lips of the internal opening. The posterior end of the vas deferens appears to be ciliated. In transverse section the lumen of the anterior portion of the duct is very small and often shows only as a line.

(iv) **Sperm Vesicles** (figs. 1, 2, 64, *ves.sem.*). The posterior end of each vas deferens opens into the anterior end of a papilla- the *sperm vesicle.* These vesicles are situated one on each side of the tail, occupying the lateral area between the posterior lateral fin and the caudal fin. The exact form and shape varies with the development of the animal. In the adult individual, when seen from the dorsal surface, the vesicle has the general form of a right-angled triangle, with the shortest side forming the anterior edge placed transversely, the larger side at right-angles to this forming the surface attached to the side of the tail, and the hypotenuse forming the outer free edge (Text-fig. J). The funnel-shaped opening of this vesicle to the exterior is placed anteriorly at the corner of the greater acute angle.

The vas deferens opens into this vesicle near the right-angle. The vesicle is covered with the ordinary epidermis of the body, which is here thick and stratified, and an underlying basal membrane. It is lined by a glandular epithelium consisting of rather tall cylindrical cells having a basal nucleus and containing numerous granules of secretion (fig. 64). The secretion of these cells possibly has an activating influence on the sperm.

In adult animals the sperm vesicles are often found filled with the long filiform spermatozoa in active movement, and bunches of spermatozoa are seen around the outer opening.

(v) **Spermatogenesis** (figs. 65 to 78). General descriptions of the testes and spermatozoa have been given by Hertwig (45) and Grassi (39), and more detailed accounts of the development of the sperm by Lee (60), Stevens (99, 101), and Bordas (5, 6). Retzius (80) has described the appearance of the fully-developed spermatozoon.

Since spermatogonia and spermatocytes in all stages of development are present in the tail cavities of an adult individual, these stages can easily be studied, after appropriate fixation (Bouin is very good), by making sections of the tail region about 4μ thick, and staining on the slide with Iron Hæmatoxylin followed by Eosin. The elements are very small and an oil immersion objective, often in conjunction with a high power compensating ocular, is necessary for their study.

Groups of *spermatogonia* in various stages are found in the testis. In the *resting condition* (fig. 65) the nucleus appears as a lightly staining network containing several chromatoid bodies. There is a small round *nucleolus* (*nucl.*) near the centre of the nucleus, and several *karyosomes* of variable shape and size placed just within the nuclear membrane. These spermatogonia are larger cells than the later stages.

Division of the Spermatogonia.

Prophase. The nuclei become clearer, and band-like chromosomes are formed. These can be counted, and there are found to be eighteen, which is the somatic (diploid) number for *Sagitta.* The nucleolus, karyosomes and nuclear membrane disappear.

Metaphase (fig. 66). The eighteen chromosomes become grouped around the equator of the spindle. This is followed by a very short—

Anaphase, and then in the final—

Telophase two kinds of daughter nuclei seem to be formed. In one form the daughter chromosomes are short and thick (fig. 67), and in the other long and thin (fig. 68). In the latter case the chromosomes appear to prepare for another prophase like the one just described, whereas in the former the nucleus passes into the network condition of a resting stage. Probably the first type with short thick chromosomes represents the last spermatogonial division. These nuclei then pass into a resting condition, and the nucleolus and karyosomes reappear. It is in this condition that groups of cells (" polyplasts ") break away from the testis and begin to circulate in the tail cavity. The cells so detached are the *primary spermatocytes* (fig. 69). Their nuclei are somewhat smaller than those of the spermatogonia, and stain lightly with hæmatoxylin. After resting in this condition the spermatocytes prepare for the maturation divisions. The *first spermatocyte division* is the *reducing division*, in which the somatic number of chromosomes is reduced to half.

First Spermatocyte Division. The karyosomes disappear and the nucleolus soon follows. Chromatin bands again appear as fine threads (fig. 70). This is the *leptotene stage*. Very early in the development of this stage many of the thread-like chromosomes often appear as more or less parallel pairs. A little later the chromosomes are seen to be definitely arranged in pairs with a tendency for the free ends of the chromosomes to be concentrated about one point on the periphery of the nucleus (fig. 71). This is the *zygotene stage*.

The pairs of chromosomes gradually come into very close contact and also contract at the same time, and the nucleus passes to the *pachytene stage*. In this stage the chromosome pairs form thick horseshoe-shaped bodies with their ends directed towards one area of the periphery of the nucleus. This stage is often called the *bouquet stage* (fig. 72). In *Sagitta* this is the longest and most characteristic stage. Each of the thick rods consists of two chromosomes lying very close together along their whole length. At this stage nine of these double (or bivalent) chromosomes can be counted.

A process the reverse to that which occurred in the zygotene stage now takes place. The loops become longer, tend to lose their polar arrangement, and spread out so as to fill the nucleus. The double chromosomes again separate into their two constituents. The nucleus increases in size and the chromosomes become less stainable and are often twisted around one another. The nucleolus again appears. This is called the *strepsitene stage* (fig. 73). It is followed by a second contraction phase in which the chromosomes become again thickened. Nine bivalents can again be counted and they finally appear in different forms, figures of eight and loops. This stage is a typical one in spermatogenesis, and is called the *diakinetic stage* (fig. 74).

The nuclear membrane now disappears, a spindle is formed and the cell prepares for the first maturation division. The nine bivalent chromosomes now become massed at the equator of the spindle and stain deeply. These chromosomes now appear as oval or dumb-bell shaped bodies. These each consist of two univalent chromosomes, orientated so that one of each pair lies towards one pole of the spindle, and the other towards the other pole. Thus the *Metaphase I* stage is reached (fig. 75). The univalent chromosomes now separate in *Anaphase I* and pass to opposite poles. Thus the primary spermatocytes have each divided into two *secondary spermatocytes*. In the nucleus of each of the latter there are nine univalent chromosomes.

Second Spermatocyte Division. The secondary spermatocytes pass rapidly through a second division. In this division there is no further reduction in the number of chromosomes. The chromosomes remain small, oval bodies, and the nucleus passes through a *Metaphase II* stage in which these chromosomes are again arranged at the equator of a spindle. Each chromosome splits into two daughter chromosomes, these moving to opposite poles in *Anaphase II* (fig. 76). The secondary spermatocytes thus divide each into two *spermatids*. In the forming nuclei of each of these nine chromosomes can be counted. The spermatids now proceed to develop into the typical spermatozoa. The nine chromosomes appear first to form a network and then contract into a mass of chromatin. The nucleus then begins to elongate and the caudal filament appears. Finally there is developed the ripe *spermatozoon* (fig. 77). These are seen in a section of the tail of the adult arranged in masses (fig. 36, *sperm.*), each group of spermatozoa having been developed from a " polyplast " of spermatocytes.

B. THE FEMALE REPRODUCTIVE ORGANS.

(i) **The Ovaries** (figs. 1, 2, 40, and 78). There is a pair of ovaries situated in the posterior end of the trunk cavity. These ovaries lie one on each side of the hind end of the intestine, and are thus separated from one another by the intestine and its dorsal and ventral mesenteries. In adult animals the intestine is compressed from side to side by the laterally-placed ovaries. Each ovary is an elongated cylindrical body about 2·0 mms. long and ·25 mm. wide in the adult individual. A surface view (fig. 78) shows each ovary to consist of a mass of eggs in varying stages of development, and along the outer side there can be made out a duct which runs a perfectly straight course back to the posterior end of the ovary to a point just in front of the transverse septum which separates the trunk and tail regions.

Transverse sections (fig. 40) show the ovary as a body of nearly circular outline covered with a thin layer of endothelium (*end.*) which is continuous on the outer side with the lining of the trunk cavity in the region of the lateral line. Thus each ovary is attached to the body wall, laterally, by a very short mesentery (*ov.m.*) formed by this endothelial layer. Eggs in various stages of development are seen, and usually from twelve to fifteen eggs in each ovary are recognisable in a section. The smallest and youngest oocytes are found along the middle of the outer side of the ovary, close up against the ducts which will now be described.

(ii) **The Ducts** (figs. 40, 78). At first sight the examination of whole preparations and of sections seems to show that there is a single duct extending along the outer side of each ovary, and opening at the level of the hind end of the ovary into a bulb-like seminal receptacle. Such a duct has been described by many authors, e.g., Krohn (55), Leuckhart and Pagenstecher (63), Keferstein (50), Hertwig (45) and Grassi (39). None of these were able, however, to find an opening from the ovary into the duct, though both Keferstein and Hertwig state that they saw spermatozoa in the duct. Keferstein thought that there must be an anterior opening to the duct, and Hertwig that the ripe eggs must enter the duct at its posterior end. All these authors thus described a single duct which was called either a "Samentasche" (sperm pouch), oviduct, or sperm-oviduct.

Stevens (100, 101) and Bordas (6A) have more recently returned to the subject, and the relation of the various structures has been made clear. A transverse section of an adult ovary shows a duct on its outer side (fig. 40). If examined carefully the inner walls of this duct will be seen to consist of cells with very indistinct outlines but with distinct and deeply-staining nuclei (fig. 40, *s.d.*). In some cases the lumen of the duct is not distinct, and one sees only an apparently solid mass of the tissue with indistinct cell outlines. This duct is the *sperm duct.* It is blind anteriorly, and acts as the "Samentasche" mentioned above. Posteriorly it opens on the *seminal receptacle.*

Surrounding this sperm duct there is clearly seen, in transverse sections, a layer of epithelium in which both the cell outlines and nuclei are quite distinct. This epithelium extends out as a double layer both above and below the ovary (in transverse section) in the form of a crescent (fig. 40, *od.*), so that it is within this crescent that we see the ovary proper. The youngest oocytes are always found within the median central part of the crescent (fig. 40, *im.o.*), and it is in this position that the true *germinal epithelium* is situated. The cells of the germinal epithelium can be distinguished even in a young individual from those of the inner wall of the crescent described above.

This lateral complex of sperm duct embedded in the crescent has been shown by Stevens to consist of two ducts, one within the other. Both of these are blind at their inner anterior ends, and both open by separate openings on the so-called seminal receptacle at their posterior ends. Except when eggs are actually passing to the exterior, the outer duct (*oviduct*) fits closely over the inner, so that the lumen of the former is not visible. It is the well-marked layer of epithelium with the dorsal and ventral extensions inwards which constitutes the wall of the outer duct. This is the true oviduct, and fertilised eggs make their way to the exterior along it. Stevens (101) describes the passage of the eggs down this duct from an examination of living material, and the author of this Memoir has seen a similar passage.

The fertilised eggs push their way by slow contractions and expansions through the wall of the duct and so become insinuated in a space, the lumen of the oviduct, between this wall and that of the sperm duct (fig. 40, 79, *l.od.*).

The eggs then move down the duct by slow contraction movements, pushing apart the walls of the oviduct and sperm duct as they go (fig. 79). On reaching the lower end of the duct the egg is passed to the exterior rather suddenly. The lower end of the duct is closed until an egg is actually passing out, except when several eggs are close together, in which case the external pore does not close completely between the passing of two successive eggs. Eggs appear to be able to push through the wall of the oviduct at any point along its length. The layers forming the portion of the oviduct wall which constitutes the wings of the crescent formation mentioned above, hardly separate at all as an egg is passing down the oviduct.

(iii) **The Seminal Receptacles** (figs. 78, *sem.rec.*, and 80). These are merely the posterior bulb-like expansions of the two ducts described above. The outer openings of the ducts are on the posterior ends of these bulbs, which lie at the sides of the body just in front of the transverse septum, and dorsal to the posterior lateral fins. The wall of these receptacles is similar to that of the duct complex, i.e., an inner wall with ill-defined cell outlines (the sperm duct), and an outer wall of well-marked cylindrical or cubical cells (the oviduct wall). On the outer surface is the ordinary epidermis of the body.

The cells immediately surrounding the outer openings of the ducts on the seminal receptacle are said by Bordas to be longitudinally striated, and he suggests that they act in the manner of a sphincter.

(iv) **Ovogenesis** (figs. 81 to 84). The ovary is a solid mass of oogonia and oocytes in various stages of development. The youngest *oogonia* are always found on the outer side of the ovary in the centre of the crescent formed by the oviduct walls. Thus the region just median to the inner wall of the oviduct is probably the true germinal epithelium. The young egg cells adhere to the wall of the oviduct during the period of oogonial development, and also through the earliest phases of the meiotic period. The oogonial divisions are quite comparable with those of the spermatogonia, and in the metaphase eighteen rod-like chromosomes are to be found.

The oogonium now becomes a *primary oocyte* and proceeds to undergo the various changes leading up to the meiotic or reduction division. The series of stages correspond to those found in the meiotic division of the primary spermatocyte described above. The nucleus passes successively through *leptotene*, *zygotene* and *pachytene* stages. In the latter stage nine thick loops can be counted as in the corresponding stage in spermatocyte development. Each of the horseshoe-shaped loops is a bivalent chromosome, and they are found bunched together to form a typical *bouquet stage* (see fig. 72 of spermatocyte). There are also several irregular deeply-staining bodies in the nuclear membrane. These become smaller and more numerous as the oocyte increases in size. Two noticeable changes now take place in the oocyte development. The growth phase of the oocyte is initiated, and the oocytes leave the region of the germinal epithelium and move towards the median portion of the ovary. The increase in size of the cell is considerable and, according to Bordas, a primary oocyte, 11μ × 22μ, reaches a size of 225μ × 195μ during this stage. The cytoplasm also changes in appearance, becoming reticular, and yolk is deposited (fig. 81, *y.g.*). Meanwhile the nucleus also increases considerably in size, e.g., from 13μ × 10μ to 101μ × 74μ, and the chromosomes pass from the bouquet condition to the *strepsitene stage.* The members of the thick bivalent loops separate, becoming elongated thin threads, which are more or less coiled round one another and scattered through the nucleus. These threads then gradually become more widely separated and less deeply stainable, finally developing into elongated bodies with many fine granular lateral branches (fig. 81). It is during this stage also that a vitelline membrane of considerable thickness is developed.

The chromosomes now undergo a second contraction (*diakinesis*), gradually becoming reduced in size. The lateral branches disappear and the chromosomes again stain deeply. We have now reached the stage where there are nine very small bivalent chromosomes (fig. 82).

Whilst the above changes have been going on, the maturing oocyte, on moving towards the median portion of the ovary, has become connected with the sperm duct by two *accessory cells*. These were observed by Grassi and others, but their rôle was discovered by Stevens (99). These cells (fig. 83) are apparently provided by the inner layer of the oviduct epithelium near the centre of the crescent described above. The outer of these cells (*o.a.c.*) remains connected with the sperm duct, whilst the inner (*i.a.c.*) sinks a short distance into the oocyte. Within these cells there is formed a passage from the sperm duct to the ovum, an opening being left in the thick vitelline membrane (*vit.m.*) at the connecting point. A spermatozoon passes from the sperm duct through this passage into the ovum at fertilisation. As this is taking place the nuclear membrane of the egg breaks down, and the nucleus, containing the nine small bivalent chromosomes mentioned above, moves to a point at the periphery of the ovum on the opposite side to that at which the spermatozoon enters. A minute spindle is now formed and the chromosomes pass through *Metaphase I* and *Anaphase I*.

This is the true meiotic or reducing division, the constituents of the bivalents separating, with the formation of the *first polar body* (fig. 84). The egg has now become a *secondary oocyte*.

A second spindle is then immediately formed at the same place, and the nine univalent chromosomes retained in the egg pass into *Metaphase II*, and *Anaphase II*, with the formation of the *second polar body*.

The nine chromosomes now left in the egg mass together and form a small nucleus, the *female pronucleus*, which moves back into the egg towards the male pronucleus which is advancing to meet it, and fusion takes place.

As soon as the spermatozoon has entered the egg, the micropyle is closed by the completion of the thick vitelline membrane, cutting off the outer accessory cell which degenerates.* The fertilised egg then begins to push its way into the oviduct, and so to the exterior as described above. The apparent ease with which an egg makes its way through the oviduct wall may be connected with the fact that the cells of the oviduct, in the immediate neighbourhood of the place through which an egg is passing, show signs of degeneration at this time.

XI. DEVELOPMENT.

The fertilisation and laying of the egg has been described in the previous section. The eggs, having been extruded, float in the sea and proceed to undergo their development. This development is rapid, and in *S. bipunctata* only about two days elapse between the laying of the egg and the hatching of the young form.

The development has been studied by various workers; Kowalevsky (53), Butschli (12), Hertwig (45), Doncaster (21), Elpatievsky (23), Buchner (9) and Stevens (101) have been the principal. The following short account of the development is taken in part from the above authors, and partly from the examination of various stages found in the plankton.

The egg is about one-fifth of a millimetre in diameter when laid, and it is covered by a firm transparent

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* The inner accessory cell is said by Buchner to fuse with the egg and to give rise to the "besondere Korper." See p. 82 below.

membrane. There is a considerable space between this shell and the egg inside. The first segmentations produce a spherical *blastula* with a well-marked *blastocœle*, the blastomeres being of equal size (fig. 85). When about fifty blastomeres have been formed, one side of the blastula becomes flattened and this side invaginates into the remainder, forming a typical *gastrula* (fig. 86). The *blastopore* (*bl.*) marks the posterior end of the animal.

The gastrulation continues until the tucked-in portion (*hypoblast, hyp.*) comes into close contact with the inner surface of the outer layer (*epiblast, epb.*), and the blastocœle is obliterated. The blastopore gradually narrows and the embryo elongates, becoming fusiform (fig. 87). The internal cavity of the gastrula is the *archenteron* (*arch.*). One of the particularly interesting points in the development of *Sagitta* is that, at this very early stage, a pair of large cells, which are the mother cells of the generative organs, make their appearance (fig. 87, *gen.c.*). These cells can easily be seen in the living gastrula, and are situated as shown in the figure, in contact with the hypoblast and lying in the archenteron nearer the anterior than the posterior end of the embryo.

Many workers on various groups of animals hold that special reproductive substance or substances separate from the general somatic substances of the body at an early stage. The case of *Sagitta* is interesting in this connection in view of the cytological work on the early developing stages by Elpatievsky (23, 24), Buchner (9) and Stevens (101). All these authors have described a stainable body (the " besondere Körper " of Elpatievsky), the derivation of which is doubtful,* which is found in the fertilised egg, and is said to pass entire into a particular cell of the 32-cell stage. This cell is the first primordial germ-cell. On gastrulation this body is said by Buchner to divide into two, one portion passing into each of the mother cells of the generative organs. Thus the cells which form the eggs and spermatozoa are distinguished from the first by the possession of this body, whatever its function may be.

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* See footnote to p 81.

After gastrulation has been completed the next noticeable feature in the development is the formation of the *cœlom*. This first appears as a pair of sac-like diverticula of the archenteron, placed antero-laterally (fig. 88, *cœl.p.*). These sacs are formed by the development of a pair of folds of the anterior portion of the wall of the archenteron. These folds grow backwards on either side of the median line (*arch.f.*). Thus the original single archenteric cavity become divided in front into three, a middle narrow portion which will form the alimentary canal, and a pair of lateral cœlomic chambers. At first, while the folds are gradually extending backwards, these three cavities all open into a single cavity posteriorly As these changes proceed the embryo grows in length and the anterior end becomes broadened.

The pair of mother cells of the generative organs are carried backwards at the posterior ends of the archenteric folds, and soon pass laterally round the tip of the folds into the lateral cœlomic cavities. Here they each divide into two cells, the members of each pair lying one behind the other (fig. 89, *gen.c.*).

The blastopore at the hind end closes completely, and an invagination appears at the anterior end of the embryo. This is the ectodermic *stomadæum*, which soon grows backwards and breaks through into the gut (fig. 89, *stom.*). The growth in length and narrowing of the embryo affects both the gut and cœlomic pouches. The archenteric folds continue to grow backwards until they reach the posterior wall of the archenteron and the inner walls of the folds become closely approximated. Thus the gut becomes completely separated from the cœlomic chambers, and has the appearance of a median septum running through the embryo (fig. 90, *gut.*). The lateral cœlomic chambers also become much narrowed, and their anterior ends, situated at the sides of the stomadæum, become separated off as a pair of distinct *head cavities* (fig. 90, *h.cav.*). These cavities soon disappear and their walls develop into the mesodermal structures, principally muscles, of the head. At a slightly later stage sections indicate various internal developments. At the anterior end the head begins to be outlined. Near the anterior border the epiblast is thick dorsally and laterally, but thin on the ventral side. The dorsal thickening develops into the *brain*. Slightly behind this the epiblast is thin dorsally but several cells thick at the sides of the stomadæum (which opens ventrally). These lateral thickenings develop into the *hood*. The masses of cephalic mesoderm unite dorsally but are separated ventrally by the stomadæal invagination.

The alimentary canal in the head is well-defined, and is entirely formed from epiblast (stomadæum). The mouth opening becomes an elongated slit on the ventral side of the head. The head now forms a distinct swelling at the anterior end, followed by a slightly constricted neck region. In this latter region the alimentary canal becomes suddenly compressed from side to side and lies more towards the dorsal surface. This marks the transition from ectodermic stomadæum to the true endodermic gut. The latter part of the alimentary canal remains for some time after hatching as an endodermic septum between the lateral mesoblastic masses.

The continued elongation of the embryo within the confines of the egg-shell results in the complete obliteration of the lateral cœlomic cavities at this stage, probably directly due to the compression produced in the curling up which the embryo undergoes. The head and tail, before hatching, slightly overlap (fig. 91). In the trunk region the ectoderm thickens considerably on the ventral side.

This thickening takes place fram a point just behind the head, backwards along the greater part of the body. The nuclei here sink in to the bases of the cells, which then proliferate rapidly and form small ganglion cells, which develop as two bands along the ventro-lateral areas. This ventral thickening is the first appearance of the *ventral ganglion* (*v.g.*). At the bases of the mesoderm cells of the body, fine longitudinally disposed muscular fibrils can be distinguished.

It is at this stage that the young *Sagitta* is hatched from the egg as a larva differing in many respects from the adult. This larva is quite transparent and is about 1 mm. long. The tail fin is present to some extent, and the animal swims by the sudden darting motion characteristic of the adult (fig. 92). The worm is still solid. The head is distinct from the body. The ectoderm thickenings which form the brain and ventral ganglion (*v.g.*) are well defined, and scattered on the surface of the body are *tactile organs* (*tact.*), with a structure similar to that seen in the adult.

Up to this stage the four genital cells, arranged as an anterior and posterior pair, are embedded in the mesoderm in contact with the endodermal septum (*end.sept.*), just behind the middle of the animal. For about two days there is not much change, except that the fin becomes larger, fin rays appear, and the body muscles develop further, the transverse striation being now visible. During the third and fourth days, however, there are some rather sudden changes by which the larval form becomes very like the adult, except in size. The beginning of this series of changes is seen in the appearance of a cavity in the mesoderm on each side of the body and in the head. The anterior part of the endodermic septum becomes thickened, but this thicker part ends sharply opposite the genital cells, thus marking off the true gut in front from the longitudinal septum of the tail behind. In the head an ectodermic fold develops, forming the *hood*, and beneath this four or five hooks (*seizing jaws*) can be seen on each side, the anterior of which is the smallest. These all increase in size, and new ones are added at the front end until the number for the species (7 to 10) is developed on each side.

The brain grows, and a pair of round ectodermal masses appear at the sides of the mouth, which develop into the *vestibular ganglia*. The eyes make their appearance as minute pigment spots surrounded by a clear area. The outer wall of the mesodermic cavities of the head at this time begin to develop into the definite bands of muscle fibres attached to the jaws and mouth. Thus the principal structures of the head are outlined. There are also great changes in the trunk region. The ventral ganglion becomes somewhat reduced in size, and the ectoderm cells both in front of and behind this body become vacuolated, especially along the lateral lines This vacuolated tissue disappears later in *S. bipunctata*.

In the tail region the caudal fin has become larger and extends further forward It is separated by a gap from a lateral fin which has appeared on each side.

The further important change which takes place at this time affects the genital cells. These cells, which up to the present have been embedded in the splanchnic wall of the mesoderm close against the endodermic septum, now move laterally across the cœlom to its somatic wall. This process takes several hours. As the cells move across, a *transverse septum* is formed between the anterior and posterior members of each pair of cells. Thus, by the time they have reached the somatic wall, a septum has been developed, dividing the body cavity on each side into an anterior (trunk) and a posterior (tail) portion. This is the condition seen in the adult. The formation of this septum also has the effect of separating the anterior from the posterior genital cell on each side. The anterior cells develop into the pair of *ovaries* and the posterior into the *testes.*

The animal may now be said to have ended its larval life, although it still differs from the adult in many points. The further changes are, however, gradual and extend over several weeks. The lumen of the alimentary canal begins to appear soon after the reappearance of the body cœlom, and as the latter becomes larger the alimentary canal is supported by a dorsal and ventral *longitudinal mesentery.* About the seventh day the posterior end of the canal bends ventrally to touch the ectoderm, and on the eighth day an *anus* is formed at the point of contact, a little in front of the transverse septum. On this day, also, the rudiment of the "*corona*" is developed as a horseshoe-shaped group of nuclei on the dorsal surface of the head a little behind the eyes. The ends of the horseshoe are directed backwards. The ventral ganglion becomes still further reduced relative to the length of the body, and takes on the typical adult appearance, the nuclei forming a closely-packed band down each side of a central mass of fibres.

With further development an *anterior pair of lateral fins* are formed, the rows of *teeth* and internal supporting *lateral plates* appear, and the hood becomes more defined.

The only organs which remain to be considered are the genital organs and their ducts.

The testes are developed by the backward extension and subdivision of the posterior pair of genital cells which, as we have seen, come to lie against the somatic wall of the anterior part of the tail cavities, just behind the transverse septum. The fully-developed testes form cylindrical masses of cells. As the animal becomes adult these testes bud off spermatocytes into the tail cavities as described above. The *vasa deferentia* each appear as a thickening of the ectoderm in the lateral line, between the posterior lateral fins and the tail fin. This thickening splits into two layers which soon separate, leaving a cavity between them. This cavity can be traced forward without a break as a very fine tube lying between the tail ectoderm and mesoderm (muscles). Thus it appears that the whole tube is ectodermal in origin. At its anterior end, which lies just behind the testis, the tube turns inwards and opens into the tail cavity. As the animal becomes mature a longitudinal groove appears on the outer side of the enlarged posterior part of the tube, and along this groove the outer opening of the duct breaks through. The enlarged posterior cavity is the *sperm vesicle.*

The pair of *ovaries* develop by a forward growth and subdivision of the anterior pair of primitive germ cells, which lie just in front of the transverse septum against the somatic wall of the trunk cavities. There are two ducts along the outer sides of the ovaries, as described above, and the development of these has been described by Stevens (101). These ducts develop from a fold or outgrowth of the mesoderm layer of the body wall. The development begins just behind the ovaries at the point where the seminal receptacles are finally formed, and extends forwards along the outer side of the developing ovary. At first only a thin layer of mesoderm cells with indistinct cell outlines is seen, this layer being continuous with the endothelium which covers the ovary. No lumen is developed as yet in the anterior portions of this mesoderm layer, but behind the ovary the mesoderm mass is more rounded in transverse section and here a minute lumen may be distinguished. It is this portion which will form the *seminal receptacle.*

This is the condition found in young forms in which there are about thirty to forty oogonia in the ovary. A section through a considerably later stage shows the thin endothelial membrane over the inner part of the ovary, and on the outer side, between the germ cells and the body wall, two well-marked layers of cells (fig. 93). These layers extend partly round the ovary as a two-layered crescent. Compared with a section of the adult (fig. 40) these layers will evidently form the walls of the future *oviduct* (*od.*). In a later stage a section shows that another tissue appears between the layers of the lateral wings of the crescent (*s.d.*). This tissue has no distinct cell outlines. It must evidently be produced by delamination or migration from the layers of the oviduct wall surrounding it.

As development proceeds this tissue extends and completely separates the outer and inner walls of the oviduct. Comparing this stage with the adult it is evident that this tissue is the rudiment of the *sperm duct* or " Samentasche." A section through the hinder seminal receptacle region of the oviduct shows that the wall here is formed by the same two layers of the oviduct wall, and is continuous with these. There is no marked lumen developed here as yet, and no external pore has been formed. The sperm duct tissue has not yet appeared in this receptacle region.

In a still older animal the oviduct with sperm duct tissue contracts, and the latter becomes a cylindrical rod, in which an irregular lumen appears a little later. The sperm duct tissue finally extends into the seminal receptacle, and the lumen continues here as a larger cavity. The outer openings of the ducts break through and the adult condition is reached. The outer openings of the oviducts are, as explained above, only obvious whilst fertilised eggs are actually passing to the exterior. Thus both the oviduct and the sperm duct are accessory mesodermal structures, not directly connected in development with the original mother cells of the ovaries.

XII. PARASITES.

Sagitta is a very voracious animal, swallowing such forms as Copepods and fish larvæ, and itself forms an important item in the food of fishes. It might be expected, therefore, that *Sagitta* would be an intermediate host for several parasitic worms. Larval trematodes, nematodes and cestodes have been recorded as parasites of this animal. In the material obtained from Port Erin, a larval nematode was the most common, although this did not occur very often. The only other parasite seen in *Sagitta* obtained from this area was a larval trematode, which was noted on only one occasion. Larval trematodes in *S. bipunctata* have been reported by Leuckart and Pagenstecher (63) and by Lebour (59); larval nematodes by Ulianin (105), Pierantoni (78) and Lebour (op. cit.); and two larval cestodes by Lebour (op. cit.).

The life histories of only two of these parasites are known. These are two trematode larvæ, the adults of which are *Derogenes varicus* (O. F. Müller) and *Pharyngora bacillaris* (Molin).

Derogenes varicus is a very common trematode, and is found in the stomachs of a large number of fishes. The larval form of this has also been found in *Harmothoë imbricata*, which appears to indicate that this animal may act as the intermediate host in shallow water, whilst *Sagitta* is the host further from the coast.

Pharyngora bacillaris is commonly found in the mackerel and in a few other fish. The late cercaria stage has been found in medusæ (Lebour), in ctenophores, and also free in the plankton (Nicoll, 75A). In this case also, therefore, several forms may act as intermediate host. The free-swimming cercaria of this parasite has been described by Lebour (59), and is of particular interest in being provided with a long tail with regularly arranged bunches of bristles.

Neither of these trematodes has been found in the encysted stage. The cercariæ appear to develop in the intermediate host to a late stage which is ready to enter the final host. The primary host into which the miracidium enters has not yet been discovered, though it is probably a mollusc. Figures of these larval forms are given in Lebour (59).

The larval Ascaris has also been described by Lebour (op. cit.), who states that it is probably the same as that noted by Pierantoni. The final host of this parasite is unknown. The appearance of this form, as found in a *Sagitta* of Port Erin material, is given in Figures 94 and 95. The parasite is found in the body cavity of the trunk of the *Sagitta*, in which it moves about slowly. The largest specimen seen was nearly half the length of the host. This nematode is a colourless worm with a very narrow body. The figured specimen was just over 4 mms. in length and 0·1 mm. in width. By clearing the whole specimen in cedar oil the general internal structure can easily be seen.

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XIV. EXPLANATION OF PLATES.

REFERENCE ABBREVIATIONS.

a.c. = Absorbent cells.
an. = Anus.
ant.f. = Anterior lateral fin.
ant.t. = Anterior teeth.
ap.p. = Apical pulp.
arch. = Archenteron.
arch.f. = Folds of archenteric wall.

b. = Brain.
b.g. = Ganglion cells of brain.
b.h = Boring hook.
bk.sh. = Back of shaft.
bl. = Blastopore.
blast. = Blastocœle.
b.m. = Basal membrane.
b.m.i. = Basal membrane of intestine.
b.p. = Basal pulp.
b.pnkt. = "Punktsubstanz" of the brain.
b.pt. = Base of point
b.s. = Amorphous basal substance.

c. = Cuticle.
c.f. = Caudal fin.
cl.a. = Clear area at base of rod of visual cell.
co. = Corona.
cœl.h. = Head cœlom.
cœl.p. = Primitive cœlomic pouch.
cœl.t. = Trunk cœlom.
col. = Collarette.
col.ep. = Columnar epithelium.
co.n. = Coronal nerve.
conn.tiss. = Connective tissue.
c.t.l. = Median connective tissue lamella.

d.col. = Dorsal column.
d.hd. = Dorsal line of attachment of hood.
d.l.m. = Dorsal band of trunk muscles.
d.m. = Dorsal mesentery.
d.n. = Dorsal nerve.

e. = Eye.
eg.hd. = Free edge of hood.
eg.sh. = Edge of shaft.
end. = Endothelium.
end.sept. = Endodermal septum.
ep. = Epidermis.
epb. = Epiblast.

e.v.sept. = Epithelium of vertical septum of tail
ext.p. = External process.

f. = Fibre of visual cell.
f.c. = Frontal commissure.
f.g = Frontal ganglion.
fib.m. = Central fibrous portion of ventral ganglion.
fin.r. = Fin rays.
f.n. = Frontal nerve.
f.p.b. = First polar body.

gang.c. = Ganglion cell.
g.c. = Glandular vacuolated cell of intestine.
g.e = Glandular epithelium.
gen.c. = Primitive generative cell.
gut. = Developing alimentary canal.

h. = Hairs of tactile body.
h.cav = Head cavity.
hyp. = Hypoblast.

i.a.c. = Inner accessory cell.
im.o. = Immature ovum.
int. = Intestine.
int.c.sp. = Inter-cellular space.
int.div. = Intestinal diverticulum.
int.m.org = Intra-muscular organ.
int.op. vas.def. = Internal opening of vas deferens.
i.s. = Blind sac from intestine.
i.t. = Inner tooth.

lab.n. = Labial nerve.
lat.l ep. = Lateral line epithelium
l.f. = Lateral fin.
l.g. = Large granular secretion.
l.l.m. = Lateral band of trunk muscles.
l.n. = Lateral nerve.
l.od. = Lumen of oviduct.
l.œ.n. = Lateral œsophageal nerve.
l.p. = Lateral plate.

m. = Mouth.
m.ad. = Adductor uncinorum muscle.
m.b. = Bicornis muscle.
m.c. = Main commissure.

m.c.l. = Complexus lateralis muscle.
m.c.o.a. = Constrictor oris alter muscle.
m.c.o.p. = Constrictor oris primus muscle.
md.nv. = Mandibular nerve.
m.d.o. = Dilator oris muscle.
m.d.v.e. = Dilator vestibuli externus muscle.
m.d.v.i. = Dilator vestibuli internus muscle.
m.e.i. = Expansus inferior muscle.
mes. = Mesentery.
m.e.s. = Expansus superior muscle.
mesob. = Mesoblast.
mesod. = Mesoderm.
m.f. = Muscle fibre.
m.i. = Muscle layer of intestine.
mo. = Primitive mouth.
m.o.b. = Obliquus capitis brevis muscle.
m.œ.c. = Circular muscles of œsophagus.
m.œ.l. = Longitudinal muscles of œsophagus.
m.o.l. = Obliquus capitis longus muscle.
m.o.s. = Obliquus superficialis muscle.
m.p.pr. = Protractor preputii muscle.
m.r.e. = Rectus colli externus muscle.
m.r.pr. = Retractor preputii muscle.
m.t.d. = Transversus dorsalis muscle.
m.t.v. = Transversus ventralis muscle.

n.f. = Nerve fibre.
no. = Notch.
nrl. = Neurilemma.
nu. = Nucleus.
nu.' = Nucleus of cell of tactile body.
nucl. = Nucleolus.
nv. = Nerve.

o. = Ovum.
o.a.c. = Outer accessory cell.
od. = Wall of oviduct.
œ. = Œsophagus.
œ.com. = Œsophageal commissure
œ.ep. = Glandular epithelium of œsophagus.
œ.g. = Œsophageal ganglion.
œ.n. = Œsophageal nerve.
œ.s. = Blind sac from œsophagus.
o.n. = Optic nerve.
o.t. = Outer tooth.
ov. = Ovary.
ov.m. = Ovarial mesentery.

p. = Pulp.
pap. = Papillæ.
p.b.s. = Proximal portion of basal substance.
p.can. = Pulp canal.
pig.w. = Pigmented wall of ocelli.
pit. = Central portion of tactile body.
p.v. = Posterior nerve from ventral ganglion.
post.f. = Posterior lateral fin.
post.t. = Posterior teeth.
prot. = Unmodified protoplasm.
pt. = Point.

r. = Rod of visual cell.
r.c.gl. = Glandular part of retrocerebral organ.
r.c.op. = Opening of retrocerebral organ.

s.d. = Sperm duct.
sec.sept. = Secondary septum.
seiz.j. = Seizing jaw.
sem.rec. = Seminal receptacle.
sept. = Septum between head and trunk.
sh. = Shaft.
sk.pl. = Skeletal plate.
sm.g. = Small granular secretion.
sp. = Space between hood and head.
sperm. = Various stages of spermatogenesis.
st.ep. = Stratified epidermis.
stom. = Stomadæum.
sw. = Swollen place in pulp.
sw.ep. = Swollen cells of epidermis.

tact. = Tactile organ.
t.cav. = Cœlomic cavity of tail.
t.l.m. = Longitudinal muscles of tail.
t.sept. = Septum between trunk and tail.
t.sh. = Top of shaft.

vas.def. = Vas deferens.
v.col. = Ventral column.
ves.sem. = Sperm vesicle.
vest.g. = Vestibular ganglion.
v.g. = Ventral ganglion.

v.hd. = Ventral line of attachment of hood.
vit.m. = Vitelline membrane.
v.l.m. = Ventral band of trunk muscles.
v.n. = Vestibular nerve.
v.o. = Vestibular organ.
v.œ.n. = Ventral œsophageal nerve.
v p. = Vestibular pit.
v.p.ep. = Epithelium of vestibular pit.
v.pl. = Ventral plate.
v.p.s. = Secretion of vestibular pit.
v.sept. = Median vertical septum of tail.
v.sept.div. = Division of anterior portion of vertical septum of tail.
w. = Wing of vestibular organ.
y.g. = Yolk granules.

All sections were drawn with an Abbe or Edinger Drawing Apparatus.

PLATE I.

Fig. 1. *Sagitta bipunctata.* The whole animal as seen against a black background. × 12.
Fig. 2. Semi-diagrammatic figure of the whole animal. The head has been drawn somewhat large in proportion to the remainder. × 10.
Fig. 3. Section of epidermis in the neck region. × 900.
Fig. 4. Epidermis in surface view. × 900.
Fig. 5. The right lateral plate, seen from the dorsal surface. × 120.
Fig. 6. Section of basal portion of a seizing jaw. × 465.
Fig. 7. Anterior teeth. × 120.

PLATE II.

Fig. 8. Posterior teeth. × 96:
Fig. 9. A seizing jaw. × 84.
Fig. 10. The tip of a seizing jaw. × 540.
Fig. 11. Transverse section of a portion of the caudal fin. × 372.
Fig. 12. Muscle fibres to show striation. × 240.
Fig. 13. A transverse section through a portion of the body wall to show the trunk muscles. × 720.

Fig. 14. A dorsal view of the entire head. × 39.

Fig. 15. A ventral view of the entire head. × 39.

Figs. 16-18. The first of a series of representative transverse sections through the head, beginning at the anterior end. This series was drawn to the same magnification under an Edinger projection apparatus. × 100.

PLATE III.

Figs. 19-26. Continuation of the series of transverse sections through the head. × 100.

PLATE IV.

Figs. 27-30. Continuation of the same series. × 100.

PLATE V.

Figs. 31-33. Continuation of the same series. × 100.

Fig. 34. Transverse section of the intra-muscular organ in the *M. bicornis*. Only the central portion of the muscle is shown, and the lower edge of the œsophagus. × 600.

Fig. 35. Transverse section through the trunk, showing the body wall and intestine. This section was cut immediately behind the intestinal diverticula. The absorbent cells are stippled. × 100.

Fig. 36. Transverse section of the tail, showing septa, vasa deferentia, and developing spermatozoa. × 110.

Fig. 37. A vestibular organ. × 120.

Fig. 38. A vestibular pit. × 720.

PLATE VI.

Fig. 39. Transverse section through a small portion of the wall of the hinder part of the œsophagus. × 1200.

Fig. 40. Transverse section through the middle of the trunk. This section shows the ovaries and ducts. In the intestinal epithelium some of the glandular cells are stippled. × 70.

Fig. 41. Horizontal section through the whole animal in the neck region to show the intestinal diverticula. × 115.

Fig. 42. Transverse section through the trunk at the level of the intestinal diverticula. × 100.

Fig. 43. Longitudinal vertical section through the anus. 180.

PLATE VII.

Fig. 44. Dorso-lateral view of the brain, ganglia, and nerves in the head (diagrammatic). The anterior part of the alimentary canal and the mouth opening are shown by broken lines. Only the right lateral œsophageal nerve and connections are shown. × approx. 120.

Fig. 45. Horizontal section through the brain and roots of the cerebral nerves (composite section). × 150.

Fig. 46. Longitudinal vertical section of the brain, cut to one side of the median plane. × 285.

Fig. 47. The ventral ganglion in surface view, with its principal nerves. × 40.

Fig. 48. Transverse section of the two main commissures, slightly anterior to their point of junction with the ventral ganglion. × 156.

Fig. 49. Transverse section through the ventral ganglion. × 156.

PLATE VIII.

Fig. 50. Surface view of a small portion of the epidermis, with some of the peripheral nerves. × 720.

Fig. 51. Longitudinal vertical section of the brain, cut along the median plane. × 285.

Fig. 52. A small portion of the ganglion cell mass of the brain. × 1080.

Fig. 53. The brain viewed from the dorsal surface (stained preparation). × 115.

Fig. 54. Surface view of a single tactile body (stained preparation). × 252.

Fig. 55. A tactile body seen from the side. The row of sensory hairs is seen from one end. × 426.

Fig. 56. Semi-diagrammatic figure showing position and form of the corona ciliata. × 27.

Fig. 57. A small portion of the corona, stained to show the nuclei of the sensory cells. × 130.

PLATE IX.

Fig. 58. A left eye from the surface. × 300.

Fig. 59. Transverse section through an eye. × 690.

Fig. 60. A single visual cell (semi-diagrammatic). × 1200.

Fig. 61. Transverse section to show the dorsal portion of the median vertical septum of the tail. × 600.

Fig. 62. Transverse section of the body through the region where the trunk passes into the tail, to show the division of the tail septum. × 74.

Fig. 63. A portion of a transverse section of the tail to show the internal opening of one of the vasa deferentia. × 384.

Fig. 64. A transverse section through a sperm vesicle at the level of its opening to the exterior. × 324.

PLATE X.

Fig. 65. Spermatogonium, resting condition. × 1200.

Fig. 66. Spermatogonial division, metaphase. × 1200.

Fig. 67. Spermatogonial division, telophase. Type with thick daughter chromosomes. × 1200.

Fig. 68. Spermatogonial division, telophase. Type with thin daughter chromosomes (after Bordas). × 1200.

Fig. 69. Primary spermatocytes. × 960.

Fig. 70. First spermatocyte division. Leptotene stage. × 1200.

Fig. 71. First spermatocyte division. Zygotene stage. × 1200.

Fig. 72. First spermatocyte division. Pachytene or bouquet stage. × 1200.

Fig. 73. First spermatocyte division. Strepsitene stage. × 1200.

Fig. 74. First spermatocyte division. Diakinetic stage. × 1200.

Fig. 75. First spermatocyte division. Metaphase I. × 1200.

Fig. 76. Second spermatocyte division. Anaphase II. × 1200.

Fig. 77. A fully-developed spermatozoon (partly after Retzius). × 1300.

PLATE XI.

Fig. 78. Right ovary in dorsal surface view. The ducts are shown in optical section, and the dorsal inward extension of the oviduct wall is omitted. × 50.

Fig. 79. Eggs entering the oviduct, as seen in the living animal. × 60.

Fig. 80. Longitudinal section through left seminal receptacle. The sperm duct is shown just open to the exterior, and spermatozoa are seen in the duct. × 280.

Fig. 81. Ovum in growth phase, with elongated, lightly-staining, branched chromosomes, and yolk granules in reticular cytoplasm. × 300.

Fig. 82. The nucleus of an ovum after the second contraction of the chromosomes (after Bordas). × 300.

Fig. 83. Portion of an egg with thick vitelline membrane and accessory cells (partly after Stevens). 600.

Fig. 84. The first polar body and second spindle (after Stevens). × 600.

PLATE XII.

Figures 85 to 90 are represented as optical sections.

Fig. 85. Blastula. × 180.

Fig. 86. Early gastrula. × 180.

Fig. 87. Late gastrula, showing genital cells. × 180.

Fig. 88. Formation of cœlomic pouches by archenteric folds. Blastopore still open. × 180.

Fig. 89. Formation of stomadæum. Genital cells divided. Blastopore closed. × 180.

Fig. 90. Head cavities formed. Backward growth of archenteric folds. × 180.

Fig. 91. The condition a short time before hatching. × 180.

Fig. 92. Newly-hatched form (after Doncaster). × 60.

Fig. 93. Transverse section of a young ovary to show the formation of the ducts (after Stevens). × 115.

Fig. 94. Larval Ascaris in host. × 5·5.

Fig. 95. Larval Ascaris, parasitic in *Sagitta*. × 30.

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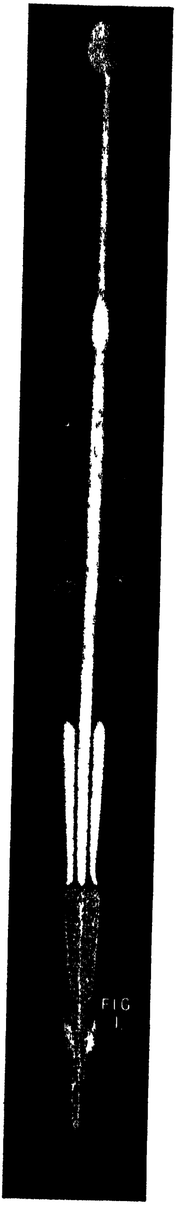
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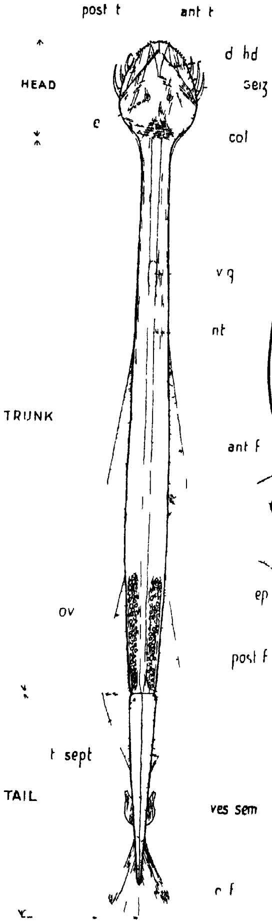

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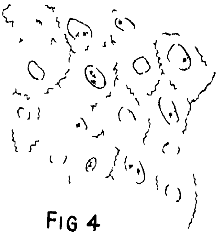
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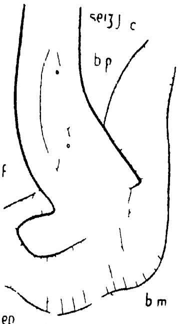

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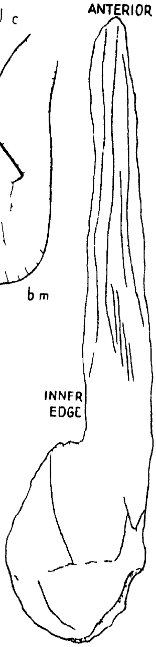

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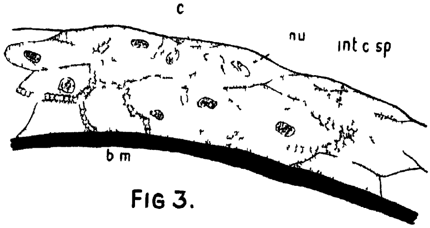

FIG 3.

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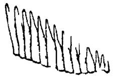

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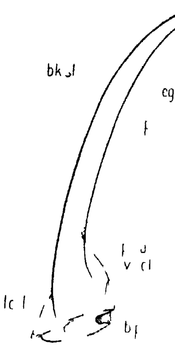

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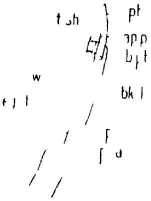

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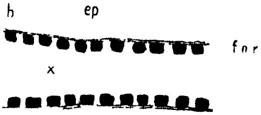

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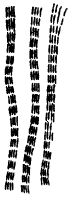

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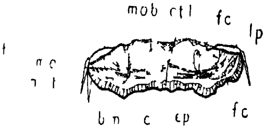

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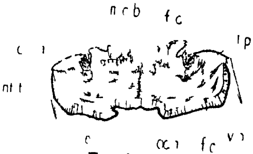

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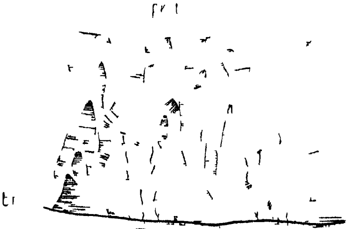

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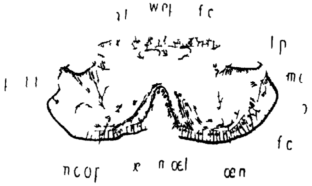

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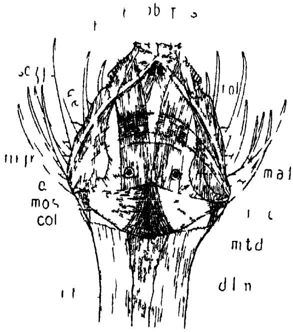

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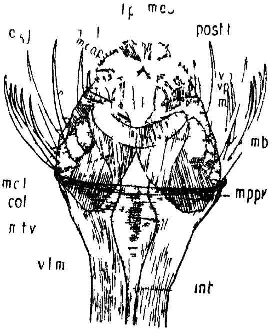

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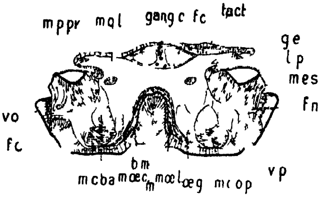

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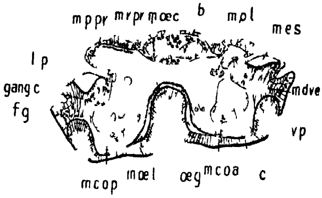

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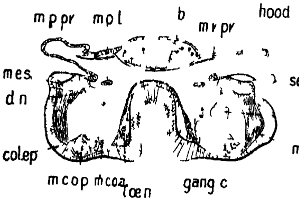

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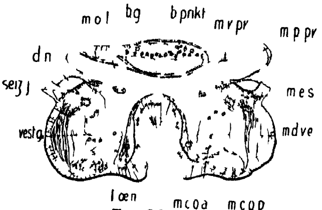

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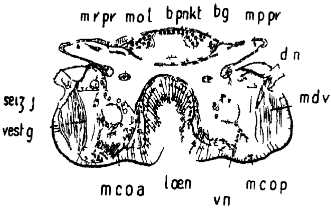

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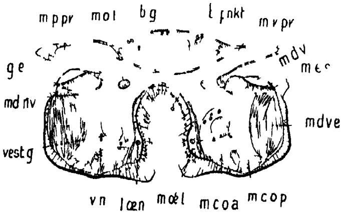

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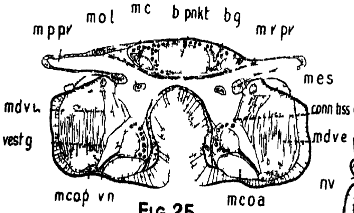

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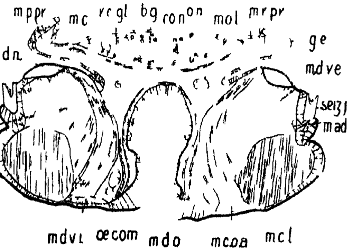

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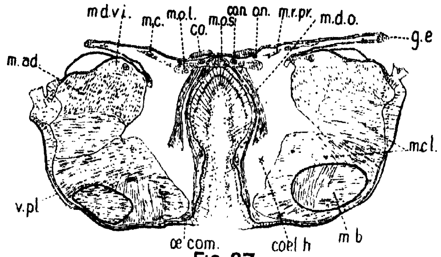

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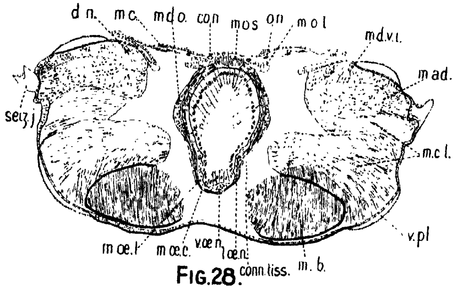

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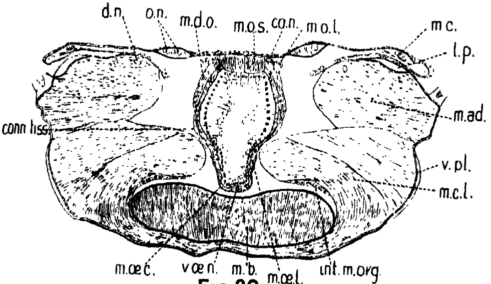

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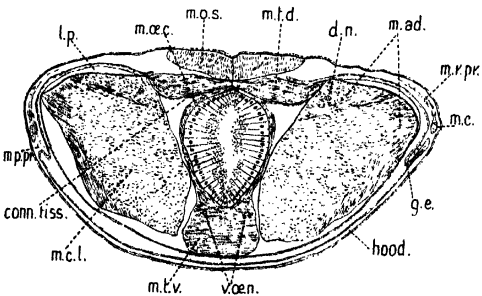

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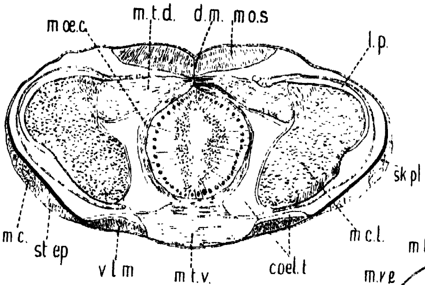

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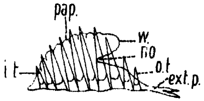

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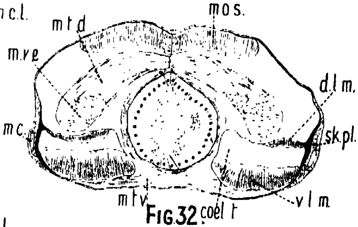

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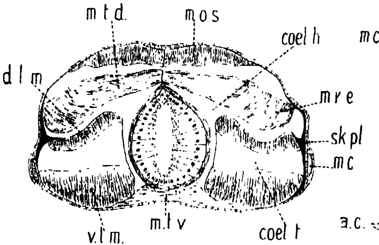

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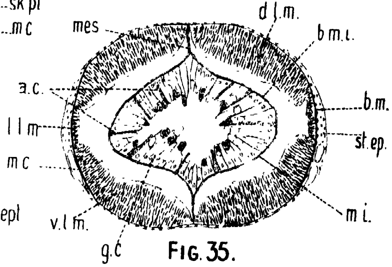

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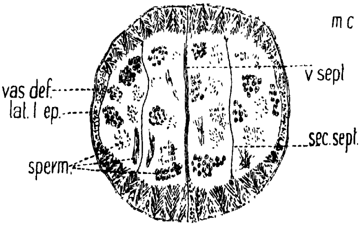

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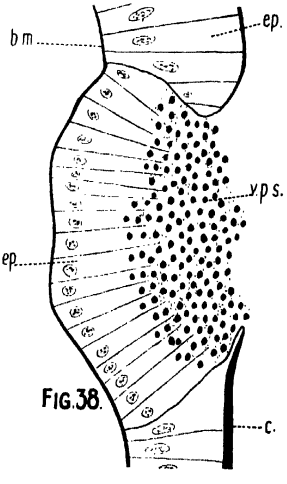

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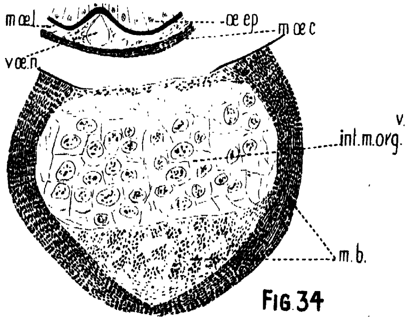

FIG 34

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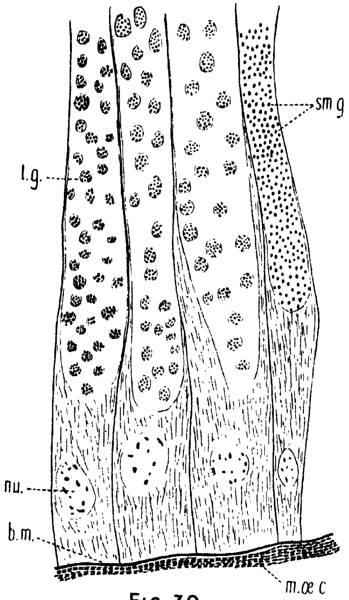

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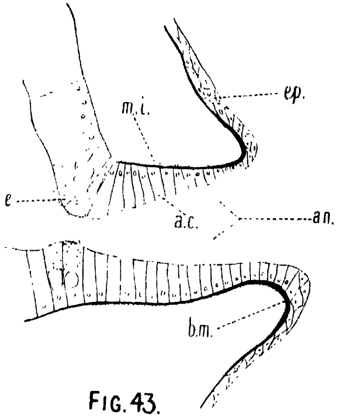

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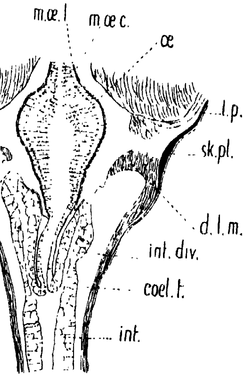

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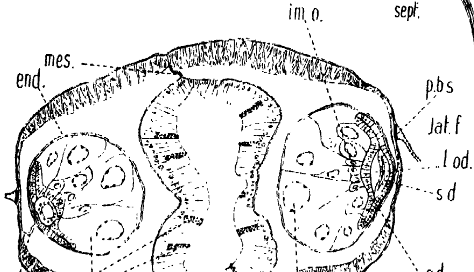

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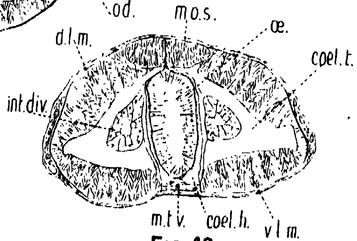

FIG. 42.

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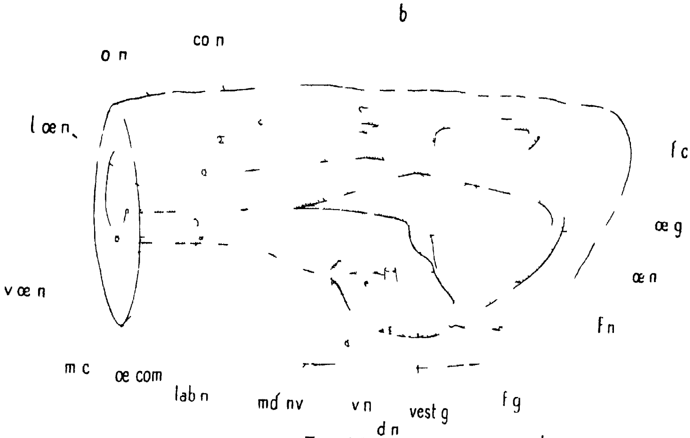

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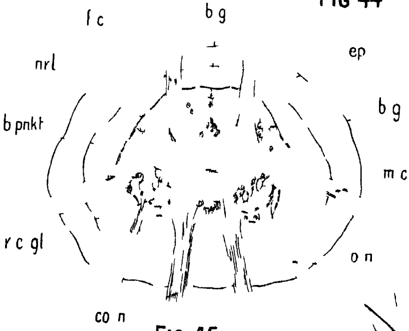

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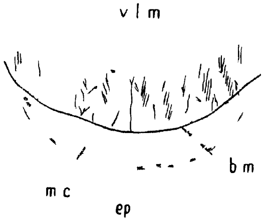

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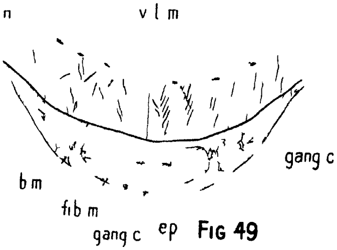

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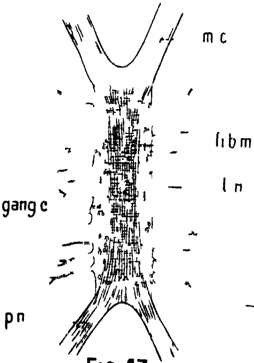

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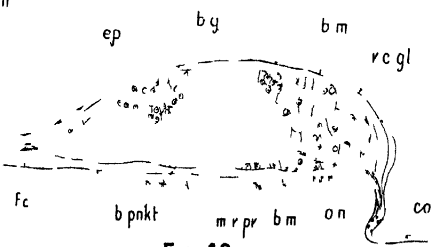

FIG 46

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SAGITTA

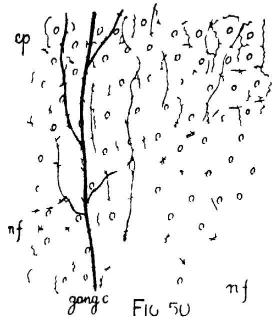
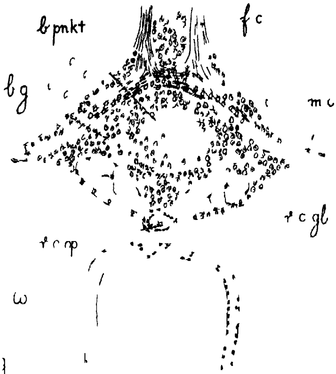


Fig 50



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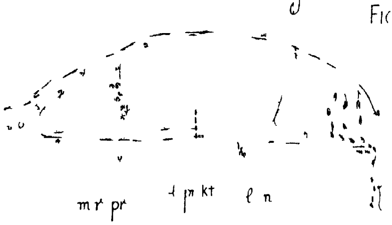

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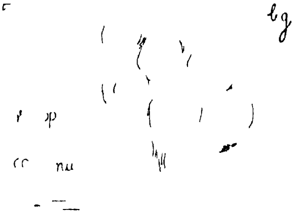

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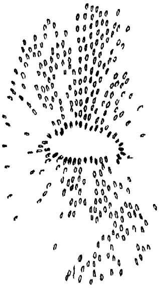

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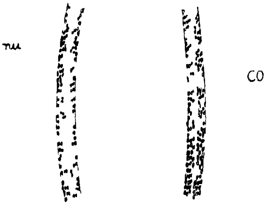

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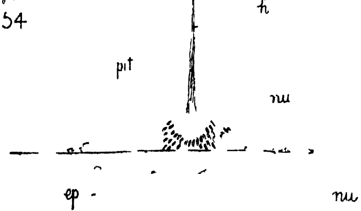

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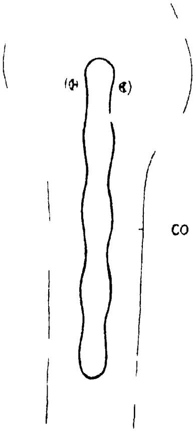

Fig 56

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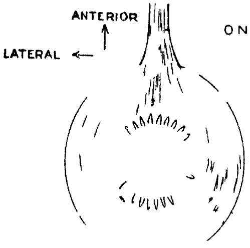

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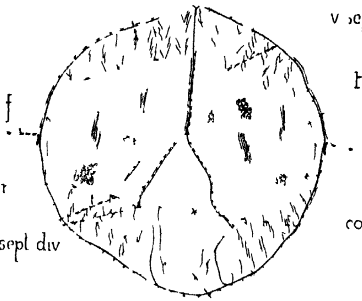
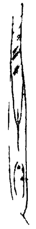


Fig 62



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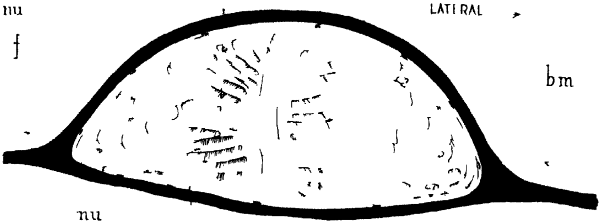

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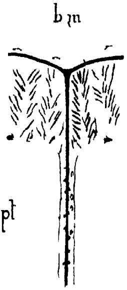

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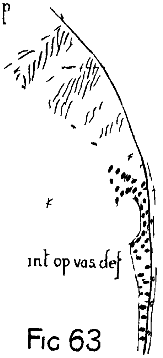

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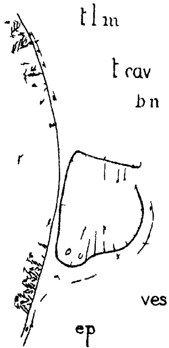

Fig. 64

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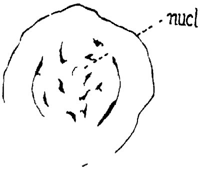

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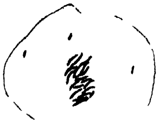

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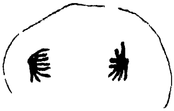

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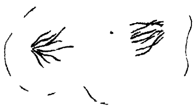

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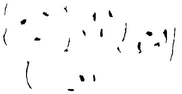

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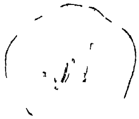

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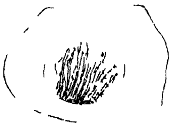
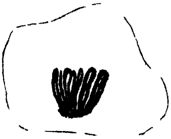


Fig 71



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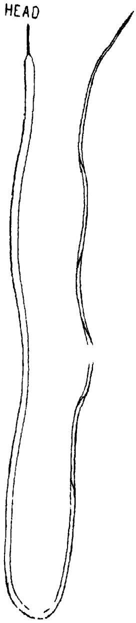
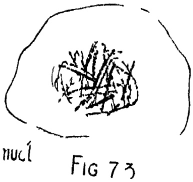


Fig 77



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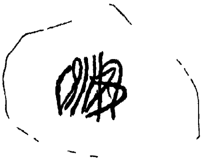

Fig 74

Fig. 75

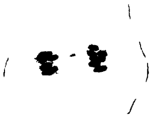

Fig 76

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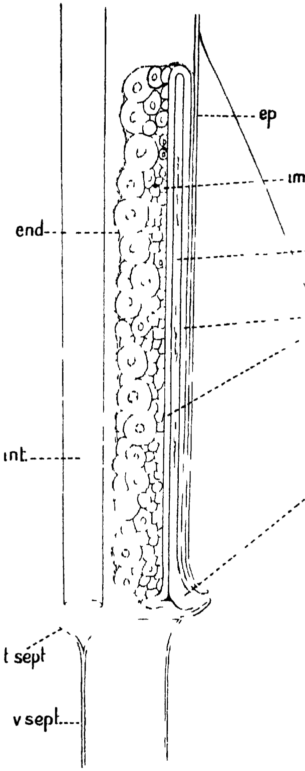

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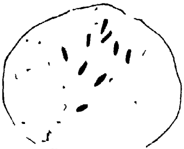

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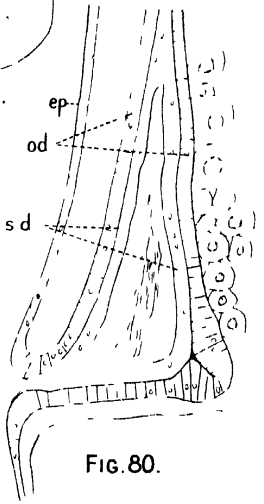

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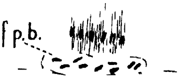

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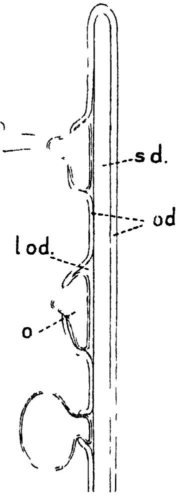

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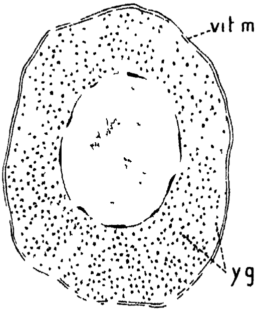

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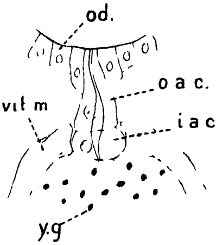

Fig. 83.

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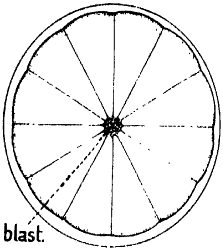

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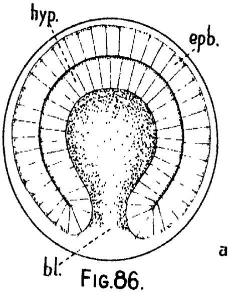

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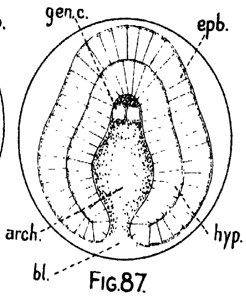

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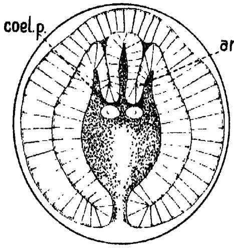

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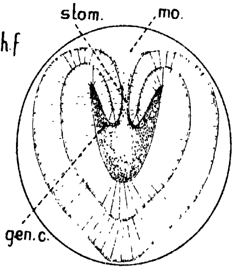

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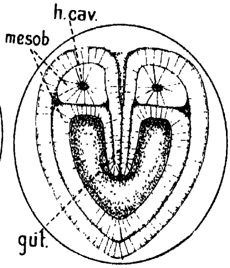

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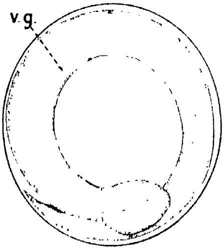

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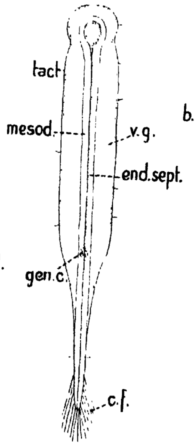

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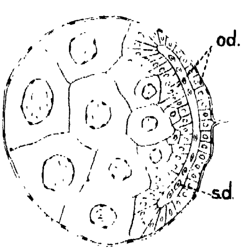

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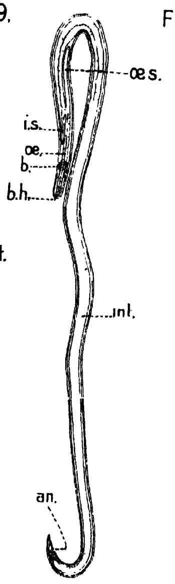

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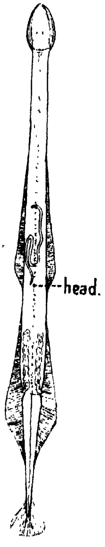

FIG. 94.

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